

COMPARATIVE MORPHOLOGY AND REDESCRIPTION OF THREE SPECIES OF *CALLIOSTOMA* (GASTROPODA, TROCHOIDEA) FROM BRAZILIAN COAST

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ABSTRACT

The morphology of *Calliostoma adpersum*, *C. depictum* and *C. hassler*, from the Brazilian coast, were studied in detail. Their anatomy has particularities that may be unique to the genus, such as: presence of an ampulla in the female; reduction or loss of the cephalic lappets; presence of a pseudoproboscis; occurrence of the intestinal loop outside the head-foot haemocoel. At species level, we conclude that *C. vinosum* is a synonym of *C. hassler*, because specimens identifiable as both species occur within a single ontogenetic series. *Calliostoma hassler* can be distinguished by: lack of the left dorsal esophageal fold, absence of a gastric spiral caecum and presence of an intestine with two wide loops. Based on anatomical evidence, we concluded that *C. depictum* is not a synonym of *C. adpersum*, differing by strongly convex whorls and a distinct suture; a marked groove near the columella; an odontophore partially covered by the mid-esophagus; absence of the pair of odontophore muscles m8a; a ventral esophageal fold of the same size as the dorsal folds; and a reduced spiral caecum with 0.5 whorl.

Key words: *Calliostoma*, comparative anatomy, Vetigastropoda, Calliostomatidae, Brazilian coast.

INTRODUCTION

The Calliostomatidae is a diverse family with a worldwide distribution and more than 250 recently described species (Marshall, 1995a). They are carnivorous, inhabit variable substrata normally associated with sessile invertebrates (Perron & Turner, 1978; Bryan et al., 1997; Hickman & McLean, 1990; Dornellas & Simone, 2011). Some recent molecular studies of Vetigastropod indicate Calliostomatidae to be closely related to Trochidae (Kano, 2008; Williams et al., 2008, 2010). In addition, the internal relationships of *Calliostoma* Swainson, 1840, is not well established and the taxonomic studies about the calliostomatid genera are restricted to some geographical regions (Clench & Turner, 1960; Marshall, 1995a, b).

The genus *Calliostoma* – type species, *Calliostoma conulum* (Linnaeus, 1781) – includes 95 species from the western Atlantic (Clench & Turner, 1960; Quinn, 1992). Previous investigations into the systematics of the genus have only used radulae, jaw and shell features (Ikebe, 1942; Clench & Turner, 1960; Quinn, 1992; Marshall, 1995a, b). The mainly characteristics

of *Calliostoma* are the presence of ampulla in females, which consist in a modification of the right kidney nephrostome; a pseudoproboscis; four pairs of epipodial tentacles; and a reduction or loss of the cephalic lappets. The radula in the subfamily Calliostomatinae has a low, reduced field of thin, highly flexible teeth with fine, serrate cusps. Calliostomatinae possess a stout, enlarged innermost marginal tooth with a heavy base and coarsely serrate hooked cusp. The serrate marginal teeth have a broad range of morphologies (Hickman & McLean, 1990).

Despite previous work on the genus, the internal anatomy of *Calliostoma* remains poorly understood and only few works described anatomical features (Randles, 1905; Fretter & Graham, 1962; Sá & Coelho, 1986; Dornellas, 2012). The relationships among calliostomatid species have proved difficult to understand, because the radular morphology and the external anatomy appear to be highly conservative within major groups. Traditional features (e.g., shell morphology) are not suitable for defining genera or subgenera, as a bewildering mosaic of intermediate character states exists (Marshall, 1995a).

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We aim to examine the external and internal anatomy of four species within the genus: *Calliostoma adpersum* (Philippi, 1845), *C. depictum* Dall, 1927, *C. hassler* Clench & Aguayo, 1939, and *C. vinosum* Quinn, 1992. In addition to the increase of specific definition of these species, which possess some taxonomical problems, this paper has also the intention of furnishing data for a future revaluation of the higher taxa, such as genus and family levels. Additionally, the proposed characters of the genus are investigated and updated and a new set of features to define the *Calliostoma* species is erected.

MATERIAL AND METHODS

Specimens were preserved in 70% alcohol extracted from their shells and dissected in a stereomicroscope with the specimen immersed in fixative. All drawings were made with a camera lucida. SEM examination of radulae, jaws and protoconch were made in the Laboratório de Microscopia Eletrônica do Museu de Zoologia da Universidade de São Paulo. The histological analysis were made in the Instituto Butantan. The specimens *in vivo* were analyzed and photographed under stereomicroscope without being extracted them from their shells. The terminology of the odontophore muscles follows Simone (2011).

Anatomical abbreviations: aa, anterior aorta; ab, bulbus aortae; af, afferent gill vessel; an, anus; ap, ampulla or urogenital papilla; bc, buccal commissure; bg, buccal ganglion; bl, buccolabial connective; bn, buccal nerve; cb, sub-esophageal connective; cc, cerebral commissure; ce, cerebral ganglion; cm, columellar muscle; cp, cerebropleural connective; cv, ctenidial vein or efferent gill vessel; cs, supra-esophageal connective; df, dorsal fold; dg, digestive gland; ef, esophageal folds; eg, esophageal gland or crop; el, esophageal papillae; em, mature spermatocyte; ep, epipodium; es, esophagus; et, epipodial tentacle; ev, esophageal valve; fs, foot sole (mesopodium); ft, foot; gi, gill; go, gonad; gs, gastric shield; hg, hypobranchial gland; il, intestinal loop; in, intestine; jw, jaws; la, left auricle; lc, spiral caecum; lf, left nephrostome; lg, labial ganglion; ln, neck lobe; lv, labial nerve; m1–m12, odontophore muscles; ma, mantle; mb, mantle border; mc, mouth sphincter; mj, jaw and peribuccal muscles; mo, mouth; mp, pericardium membrane; mt, transversal muscle; ng, nephridial gland; oa, opercular pad; oc, anterior odontophore cartilage;

od, odontophore; ol, out lip; om, ommatophore; on, optic nerve; oo, oogonia; op, operculum; os, osphradium; ov, oocyte; oy, mature oocyte; pa, papillae; pb, pseudoproboscis; pc, pericardium; pd, pedal cord; pe, pedal ganglion; pf, anterior furrow of pedal glands; pl, pleural ganglion; pm, cerebropedal connective; po, posterior odontophore cartilage; prs, posterior end of radular sac; ps, papillary sac; ra, radula; re, rectum; rk, right kidney; rs, radular sac; ru, right auricle; rv, right pallial vein; sa, posterior aorta; sc, subradular cartilage; sg, skeleton of gill; sm, subradular membrane; sn, snout; st, stomach; ta, statocyst; te, cephalic tentacle; ti, typhlossole; tn, tentacular nerve; to, tissue on radula; tr, trabeculae; um, suspensory membrane; ve, ventricle; vf, ventral fold; vt, transverse pallial vessel.

Institutional abbreviations: FSBC I, Invertebrate Collection, Florida Marine Research Institute, St. Petersburg, Florida; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MfN, Museum für Naturkunde der Humboldt-Universität zu Berlin; MORG, Museu Oceanográfico Rio Grande, NHM, Natural History Museum, London; NMNH/USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; MZSP, Museu de Zoologia da Universidade de São Paulo.

RESULTS

Genus *Calliostoma* Swainson, 1840
(For further discussion and synonymy, see Marshall (1995a))

Calliostoma adpersum
(Philippi, 1851)

Figs. 1–8, 36–39, 45–47, 54–77

Trochus eximius Reeve, of Philippi, 1844: 17, pl. 4, fig. 7 (*non* Reeve, 1842).

Trochus adpersus Philippi, 1849: pl. 32, fig. 8; 1851: 217.

Ziziphinium adpersum Beck, *in litteris*, Philippi, 1851: 218.

Calliostoma adpersum: Tryon, 1889: pl. 18, figs. 1, 2; 1890: 367; Quinn, 1992: 107, figs. 98–100, 121; Sunderland & Sunderland, 1996: 16; Salvador et al., 1998: 1016; Abbott & Dance, 1986: 38, fig.; Rosenberg, 2009; Souza et al., 2010: 306.

Calliostoma (Kombologion) adpersum: Clench & Turner, 1960: 46, pl. 30; Rios 1970: 25, pl. 4; 1975: 23, pl. 5, fig. 58; 1985: 21, pl. 9, fig. 84; 1994: 33, pl. 9, fig. 95; 2009: 50, fig. 108; Regteren Altena, 1975: 10.

Type Material: Not found.

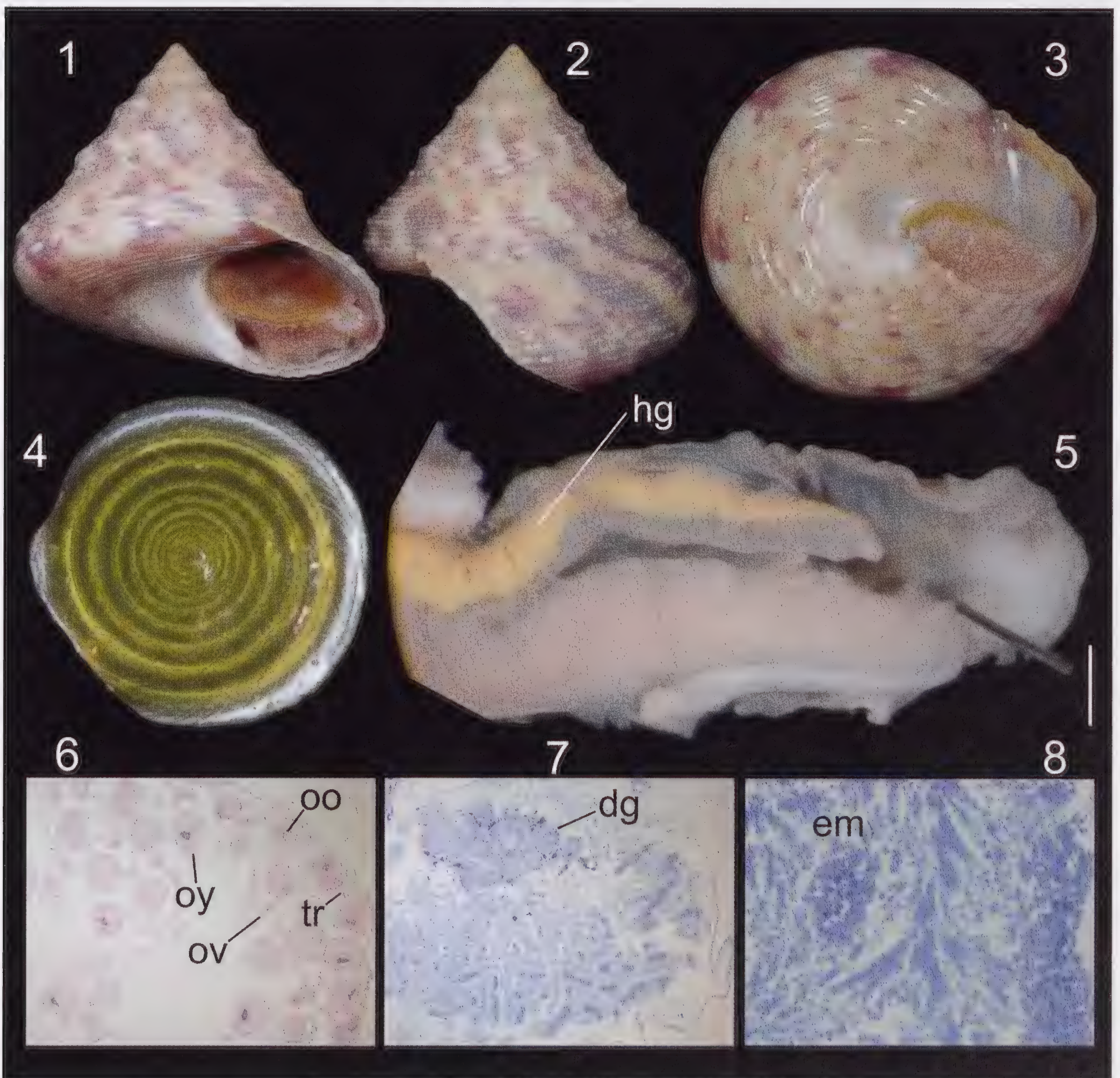
Type Locality: Brazil.

Remarks

According to some authors (Clench & Turner, 1960; Quinn, 1992), the type specimen of *Calliostoma adpersum* was deposited in the MfN, but is likely lost. The type locality was given only as Brazil by Philippi. Later, Clench & Turner (1960) "restricted" [ICZN Code Recommendation 76A: "ascertaining or clarifying"] the

locality to Praia do Leste, Ilha Guaíba, State of Rio de Janeiro. A neotype designation would take precedence over this.

We will not assign a neotype for *C. adpersum* because the search for the holotype is still ongoing. According to Dance (1986: 222) "Philippi's specimens described in his *Enumeratio Molluscorum Siciliae* (1836–44) and some others in the Berlin Museum [MfN]. Some types in the Brit. Mus. [Natural History Museum, London]. Presumably the coll. made after 1851 is in Santiago Mus. Chile". We only checked the holdings of the MfN and the NHM.

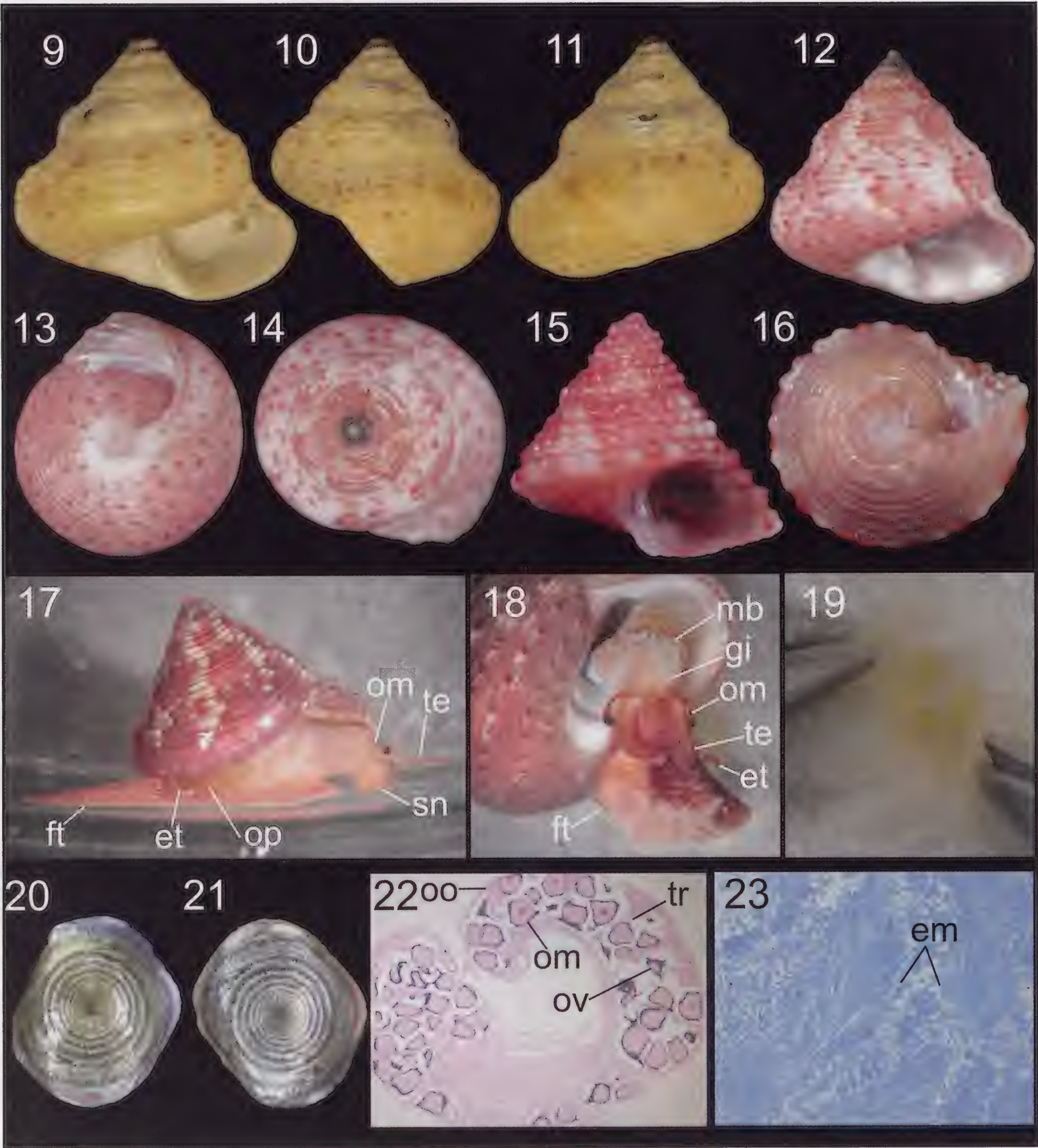


FIGS. 1–8. *Calliostoma adpersum*. FIGS. 1–3: Shells in frontal, lateral and umbilical views, MZSP 94332 (length 16.5 mm); FIG. 4: Operculum internal view, MZSP 24117 (diameter 5.6 mm); FIG. 5: Pallial cavity, ventral-inner view, MZSP 38193 (scale bar = 1 mm); FIG. 6: Ovary, MZSP 38190; FIGS. 7, 8: Testis, MZSP 63562 (HE; 5 μ m).

Diagnosis

Shell flat sided with flattened keel at whorl periphery. Foot highly papillate, light brown-

ish colored. Orange hypobranchial gland on female. Ventral esophageal fold twice as larger than dorsal folds. Spiral caecum with 1.5 whorls.

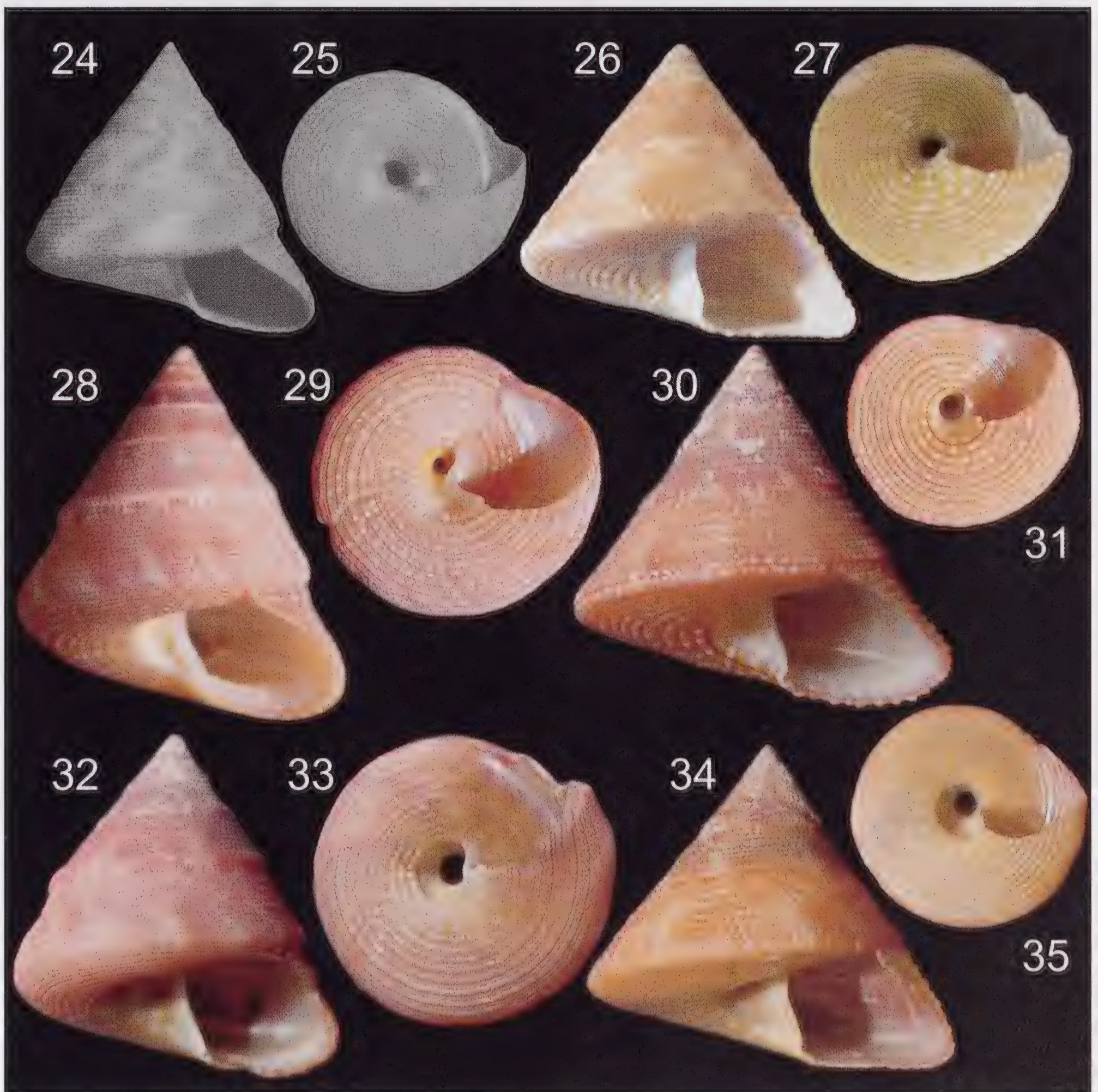


FIGS. 9–23. *Calliostoma depictum*. FIGS. 9–11: Holotype NMNH 152267 (length 10 mm), courtesy NMNH; FIGS: 12–14: Shells in frontal, umbilical and apical views, MZSP 66727 (length 13.3 mm); FIGS. 15, 16: Shells of juveniles in frontal and umbilical views, MZSP 92390 (length 2.5 mm); FIGS. 17, 18: Living specimen, MZSP 92413 (length ~10 mm); FIG. 19: Jaws in situ, ventral view, MZSP 41575 (length ~1 mm); FIG. 20: Operculum, internal view; FIG. 21: Same, external view, MZSP 41575; FIG. 22: Ovary, MZSP 47575; FIG. 23: Testis, MZSP 41575 (HE; 5 µm).

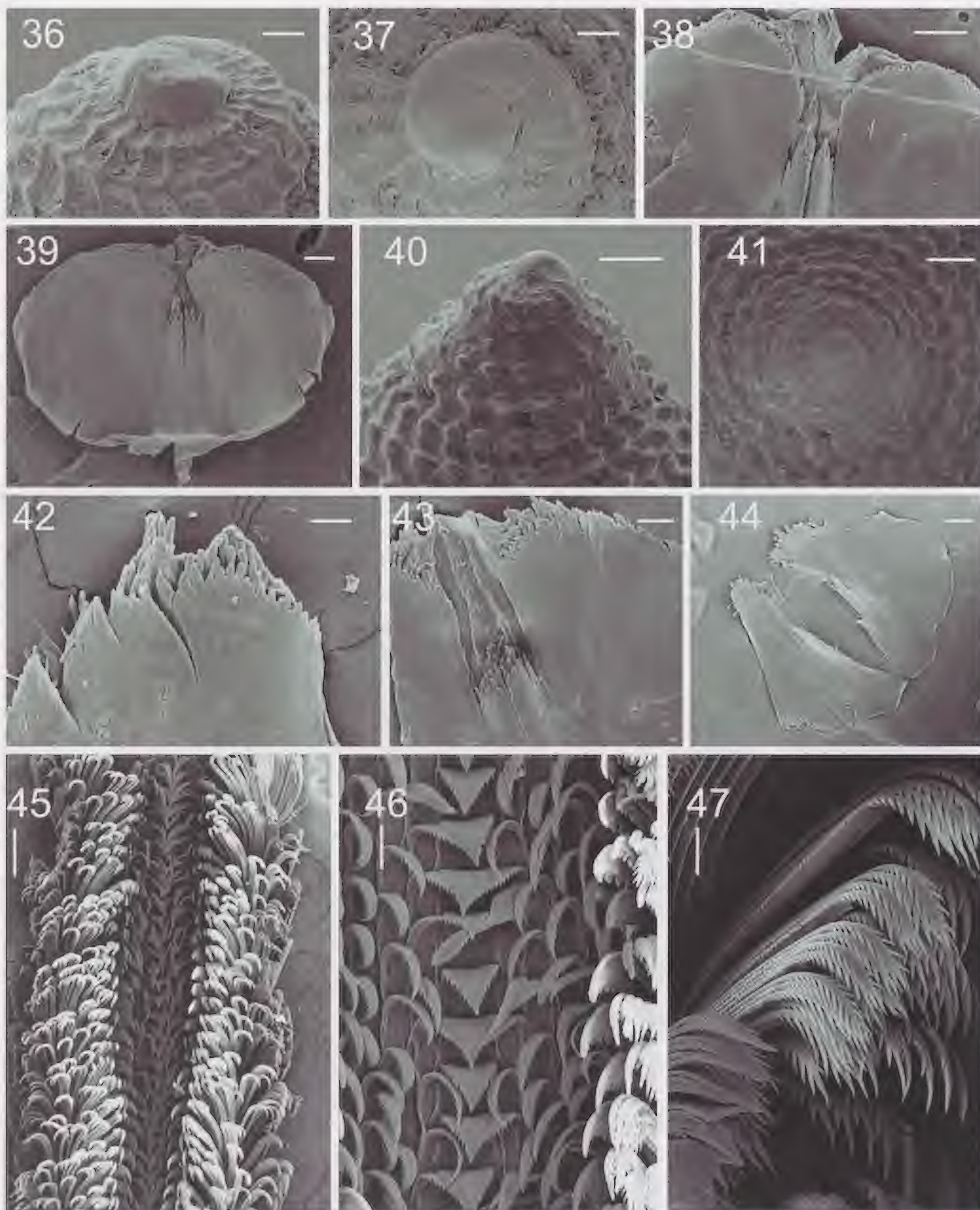
Description

Shell (Figs. 1–3): up to eight whorls and 20 mm in height and diameter; imperforate and grooved (Fig. 3), depressed trochoid, flat-sided with flattened keel on last adult whorl. Color ivory, with large axially aligned irregular brownish red or purple blotches; basal portion with irregularly spaced, fine reddish brown or purple spots on cords. Protoconch (Figs. 36, 37) of one whorl, light-colored, smooth.

Suture indistinct. Umbilical area iridescent, with a lengthened depression to left of columella. Teleoconch sculptured by beaded spiral cords; superior cord more pronounced along whorls. Last adult whorl with 18 beaded cords. Keel with two broad beaded cords, with two smaller cords between them. Basal surface of last adult whorl with 12 smooth and large cords. Thin ribs (Fig. 36) between beaded cords in first teleoconch whorl. Spire angle $\sim 80^\circ$. Aperture subquadrate; proso-



FIGS. 24–35. Shells of *Calliostoma hassler* in frontal and umbilical views. FIGS. 24, 25: Holotype MCZ 104554, extracted from Clench & Turner (1960) (length 30 mm); FIGS. 26, 27: Holotype of *C. vinosum* MORG 29294 (length 13.5 mm), courtesy MORG; FIGS. 28, 29: MZSP 37264 (length 30 mm); FIGS. 30, 31: MZSP 37264 (length 17.5 mm); FIGS. 32, 33: MZSP 34885 (length 27.5 mm); FIGS. 34, 35: MZSP 34855 (length 20 mm).



FIGS. 36–47. Protoconch, jaws and radulae in SEM. FIGS. 36, 37: *Calliostoma adpersum* protoconch in slanted and apical views, MZSP 41738 (scale bars = 60 μ m); FIGS. 38, 39: Same, jaws in ventral view, MZSP 24117 (scale bar = 200 μ m); FIGS. 40, 41: *Calliostoma depictum* upper whorls with oblique and apical views, MZSP 66835 (scale bars = 200 and 300 μ m); FIGS. 42, 43: Same, jaws in detail of anterior area, MZSP 91749 (scale bars = 40 and 60 μ m); FIG. 44: Jaws of *Calliostoma hassler*, ventral view, MZSP 34885 (scale bar = 300 μ m); FIG. 45: Radula of *Calliostoma adpersum*, whole view of middle region, MZSP 38190 (scale bar = 200 μ m); FIG. 46: Same, detail of central area, MZSP 38193 (scale bar = 60 μ m); FIG. 47: Same, detail of marginal teeth, MZSP 24117 (scale bar = 40 μ m).

cline ($\sim 45^\circ$ with columellar axis). Columella arched, truncate at base.

Head-Foot (Figs. 54–58): total length slightly more than half whorl when contracted and twice that when extended. Head bulging approximately in middle region of head-foot. Snout wide, cylindrical; distal end wider than base; distal surface plane, papillated, with papillae longer in edge and smaller close to mouth. Each papillae long, cylindrical, with rounded tip. Outer lip of mouth

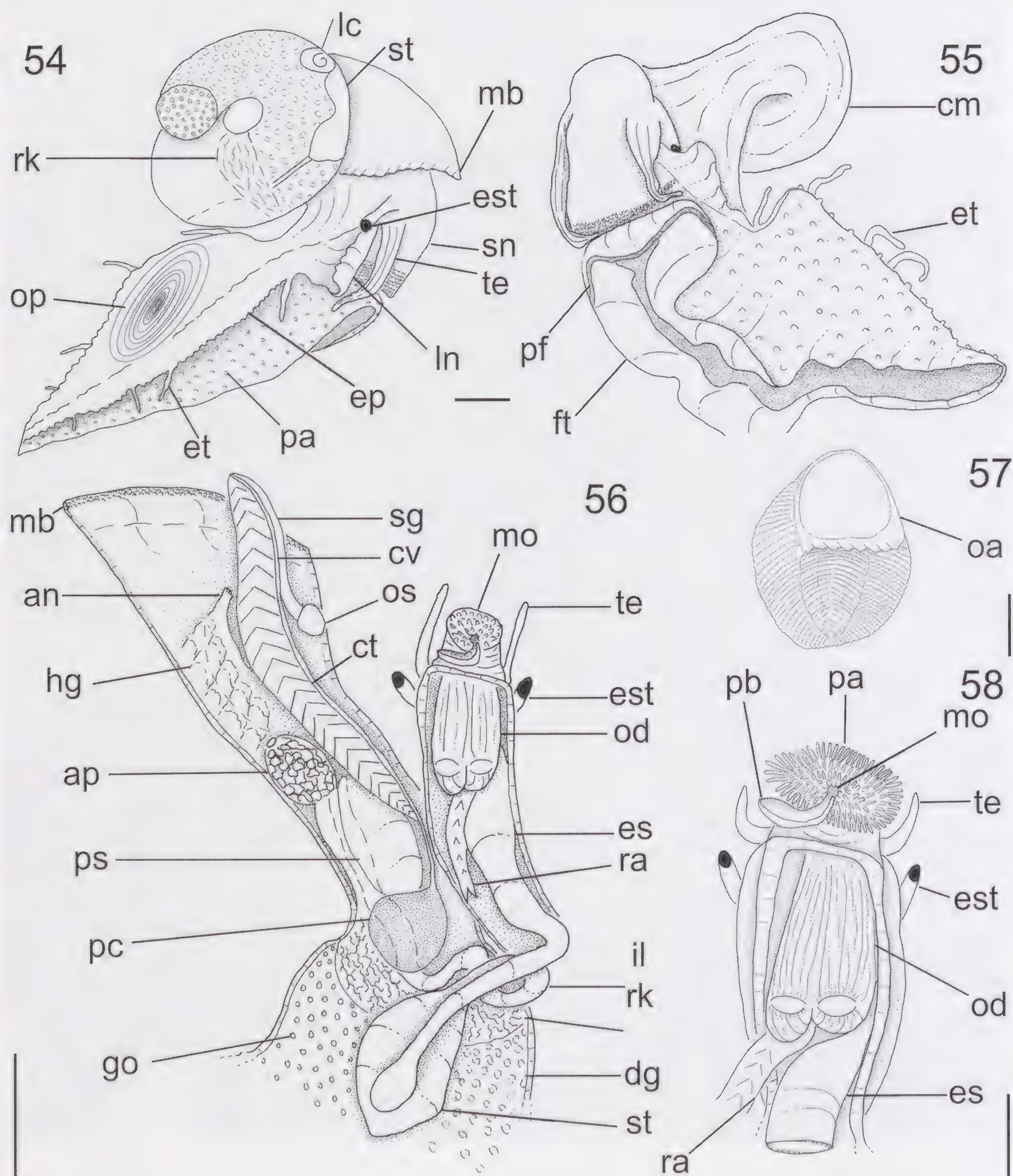
(Fig. 58) with pseudoproboscis. Mouth longitudinal, located in middle portion of ventral surface of the snout. Pair of cephalic lappets absent. Cephalic tentacles (Figs. 54–56, 58: te) $\sim 35\%$ longer than snout, sometimes asymmetrical in relation to one another, covered by small papillae, dorso-ventrally flattened, grooved, narrowing gradually up to a lightly pointed tip. Ommatophore on outer base of cephalic tentacles $1/5$ of tentacles length. Eyes dark, round, occupying anterior edge of ommatophore.



FIGS. 48–53. Radulae in SEM. FIG. 48: *Calliostoma depictum*, whole view in middle region, MZSP 91749 (scale bar = 200 μm); FIG. 49: Same, detail of central area, MZSP 41575 (scale bar = 60 μm); FIG. 50: Same, detail of central area and marginal teeth, MZSP 92320 (scale bar = 60 μm); FIG. 51: *Calliostoma hassler*, detail of central area, MZSP 69424 (scale bar = 200 μm); FIG. 52: Same, detail of rachidian and lateral teeth, MZSP 69424 (scale bar = 60 μm); FIG. 53: Same, detail of marginal teeth, MZSP57485 (scale bar = 90 μm).

Foot thick, occupying half of total head-foot length; dorsal region light brown densely papillated. Foot divided into mesopodium and epipodium. Epipodium (Fig. 54: ep) surrounding latero-dorsal region of mesopodium, equidistant from sole and base of ommatophores.

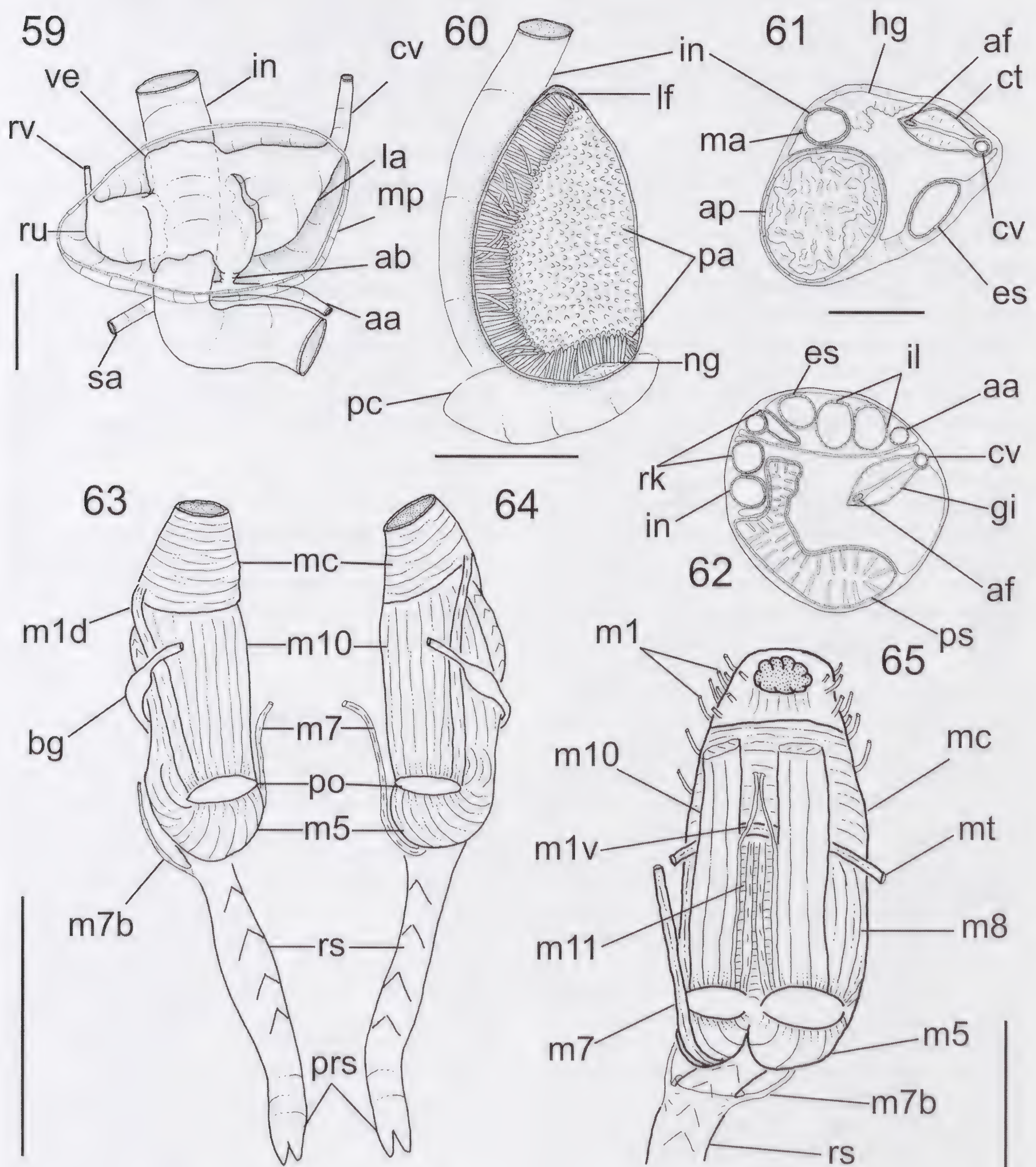
Opercular pad (Fig. 57) rounded, located in median dorsal region, with free edge on posterior area; posterior end with several chevron furrows, apex pointed toward posterior and two pairs of longitudinal furrows on median line. Furrow of pedal glands along entire anterior



FIGS. 54–58. Anatomy *Calliostoma adpersum*. FIG. 54: Head-foot, right side and visceral mass; FIG. 55: Same, anterior-slightly left view; FIG. 56: Pallial cavity roof, head, head-foot haemocoel and visceral mass, ventral view; FIG. 57: Opercular pad, dorsal view; FIG. 58: Head and haemocoel, ventral view, foot extracted. Scale bars = 2 mm.

edge of foot (Fig. 55: pf); single aperture of pedal glands located in median region of this furrow. Anterior third of epipodium formed by neck lobe (Figs. 54, 55: ln): one pair of wide horizontal flexible flaps. Remaining 2/3 of epipodium relatively low, thick; 4 pairs of slender tentacles (Figs. 54, 55: et) inserted on

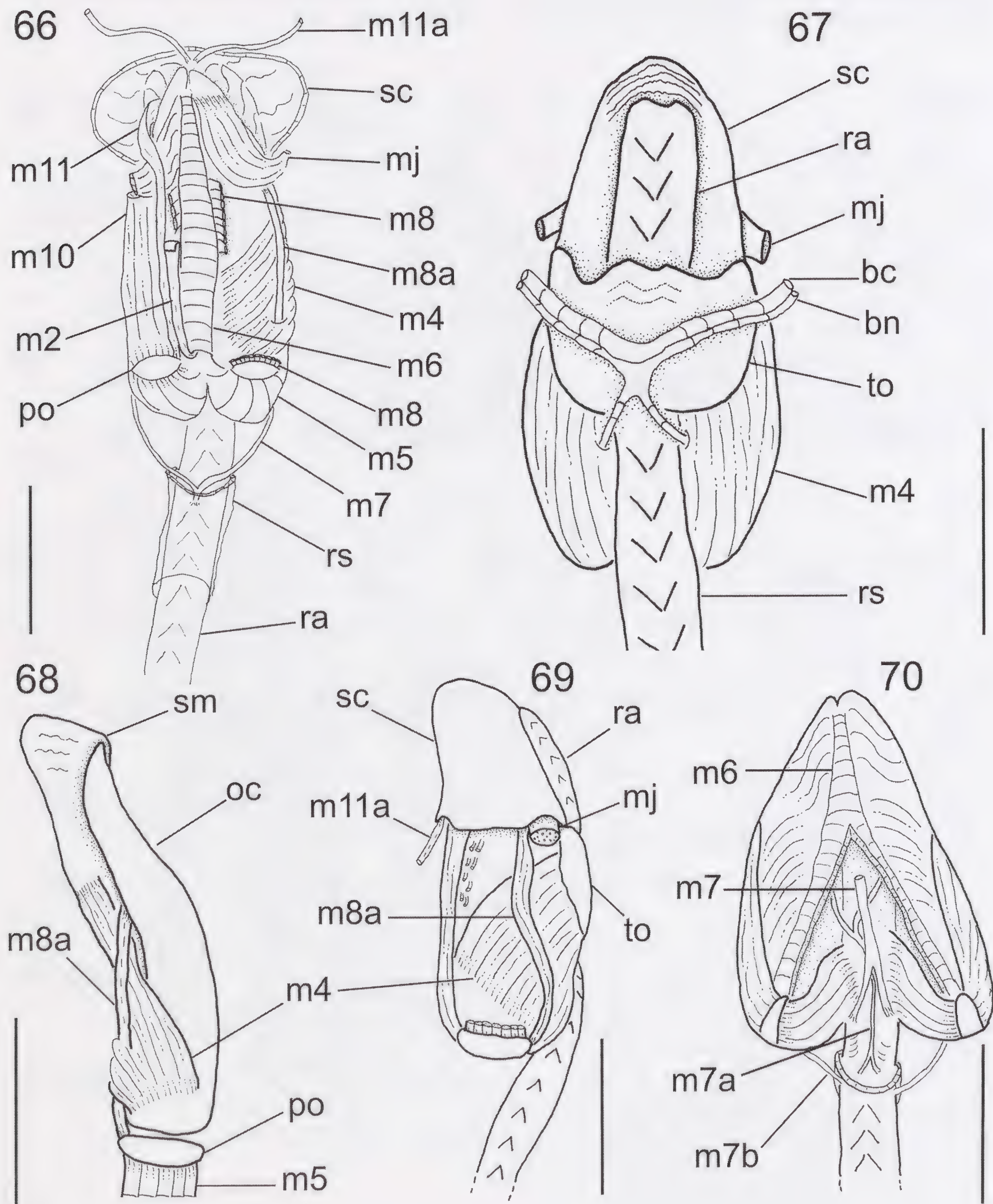
each side at distal edge. Epipodial tentacles located equidistantly, well-spaced from each other, distributed symmetrically on both sides along epipodium; tentacles shorten towards posterior region. Pair of columellar muscles thick, 1/4 whorled and fused with each other along median line.



FIGS. 59–65. Anatomy *Calliostoma adpersum*. FIG. 59: Pericardium, ventral-inner view, ventral walls and kidneys removed; FIG. 60: Papillary sac opened longitudinally, ventral-inner view, right kidney removed; FIG. 61: Transverse section in middle of ampulla region; FIG. 62: Transverse section in middle of right kidney (scale bars = 1 mm); FIGS. 63, 64: Buccal mass in right and left views; FIG. 65: Buccal mass in ventral view (scale bars = 2 mm).

Operculum (Figs. 4, 54): about 6 mm in diameter and 12 whorls, closing entire aperture; thin, with a central nucleus. Corneous, yellowish gold in color. Inner side convex, outer side concave.

Mantle Organs (Figs. 5, 56): pallial cavity of 3/4 whorl. Mantle border (Fig. 56: mb) thick, white; anterior end papillated, occupying 1/3 of mantle border. Gill located on left side of



FIGS. 66–70. Odontophore *Calliostoma adpersum*. FIG. 66: Ventral view, subradular cartilage opened longitudinally and deflected, m8 and m10 of left side removed; FIG. 67: Same, dorsal view; FIG. 68: Buccal mass, right side in lateral view, m8 and m10 removed, subradular membrane and m5 deflected; FIG. 69: Left view, m5, m8 and m10 removed; FIG. 70: Ventral view, m6 opened longitudinally along median line. Scale bars = 2 mm.

pallial cavity, measuring $3/4$ of its length and projecting anteriorly and sustained by rod of gill and suspensory membrane (Fig. 56: sg). Anterior end of gill narrow, with pointed tip. Afferent gill vessel $\sim 3/4$ of gill's length, originating in transverse pallial vessel and running on distal region of central axis of gill. Transverse pallial vessel $\sim 1/5$ of afferent vessel length, originating in left nephrostome and discharging in afferent gill vessel. Ctenidial vein (efferent gill vessel) 35% longer than afferent vessel, running on basal region of central axis of gill; posterior end of vein ($1/10$ its length) free from gill filaments, lying parallel (on the left) to afferent vessel up to the pericardium. Hypobranchial glands (Figs. 5, 56: hg) on both sides of rectum; undeveloped and white in male; thicker and orange in female.

Rectum occupying $1/4$ of pallial cavity width, sigmoid; posterior region under kidneys. Anus siphoned, preceded by pleated and short free end, located on anterior right side of pallial cavity, close to mantle border. Kidneys $\sim 1/3$ of rectum length, located on posterior region of pallial cavity; right kidney modified on females (see below).

Visceral Mass (Figs. 7, 54, 56, 72): pericardium and posterior portion of right kidney exposed in pallial cavity roof. Stomach and spiral caecum (Figs. 54, 72) $1/3$ whorl posterior to pallial cavity. Digestive gland on left side and gonad on right side (Figs. 7, 56: dg, go), both posterior to right kidney.

Circulatory and Excretory Systems (Figs. 56, 59–62): pericardium located between pallial cavity and visceral mass (Fig. 56: pc), close to median line and immediately posterior to kidneys. Left side of pericardium receiving ctenidial vein and right side receiving right pallial vein (Fig. 59: cv, ru). Ventricle $1/3$ of pericardium volume; surrounding rectum and flanked anteriorly by left auricle (ventral, triangular, of $1/3$ of pericardium volume) and posteriorly by right auricle (weak, smaller than left). Bulb of aorta (Fig. 59: ab) emerging from left end of ventricle and forming anterior and posterior aortas (Fig. 59: aa, sa). Anterior aorta running forward to end in series of sinuses in both head and foot. Posterior aorta running up to visceral hump.

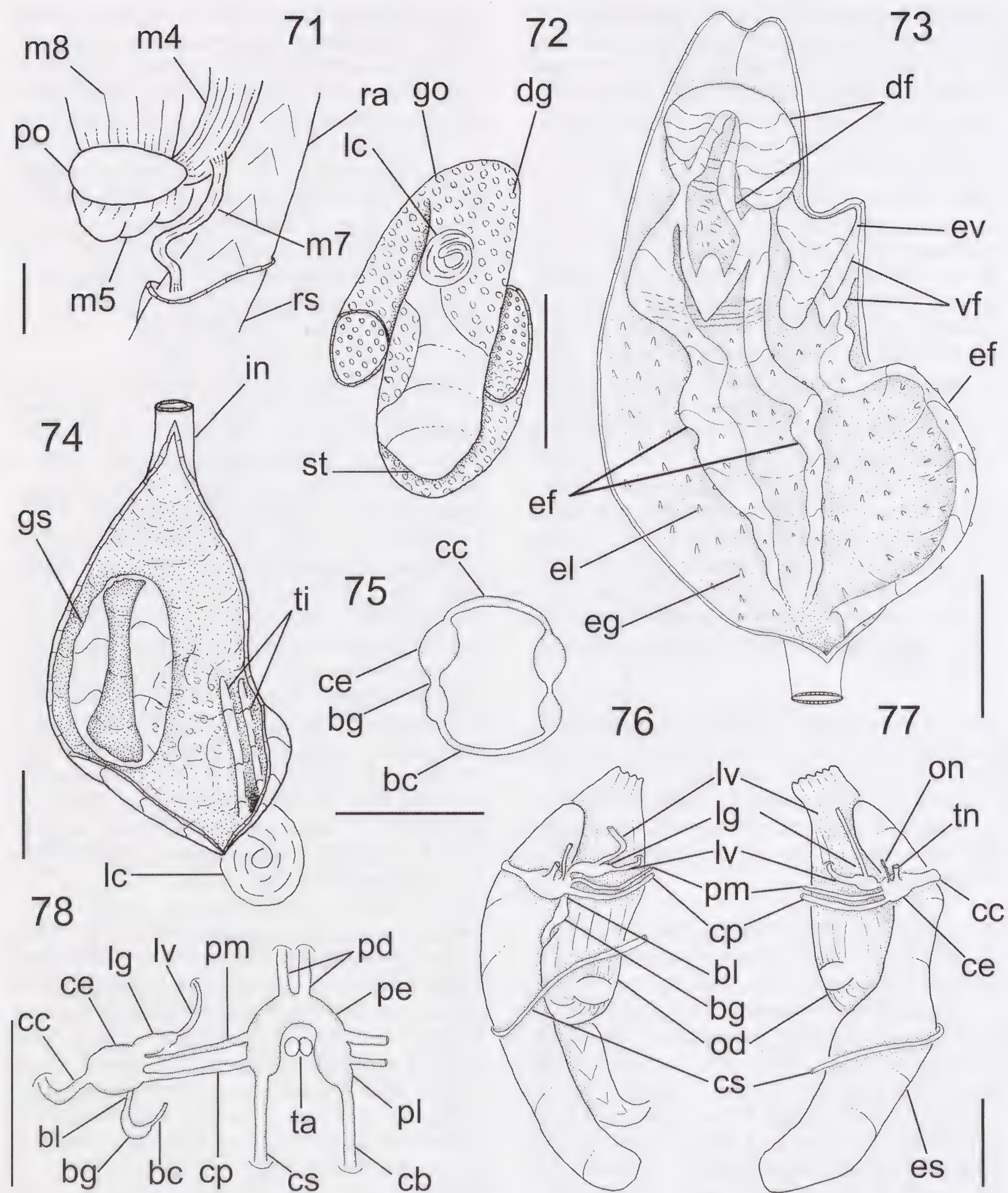
Papillary sac (Figs. 56, 60, 62: ps), or left kidney, $1/3$ of rectum length; base oval, wide, gradually narrowing towards anterior portion, ending at left nephrostome; inner wall covered with numerous thin, long papillae; posterior end

connecting with pericardium by nephridial gland (Fig. 60: ng), as special thickening of tissue.

Right kidney (Fig. 56: rk) divided into two regions. Anterior region a hollow tube $1/3$ of rectum length and $1/2$ the width of the papillary sac in males. In females ampulla, or urogenital papilla, (Figs. 56, 61: ap) large (75% larger than papillary sac), oval, hollow, filled by mucus. Posterior region spreading around visceral mass immediately beneath mantle, encircling inner surface of columellar muscle. Kidney expanding ventrally to cover half of right surface of adjacent visceral hump (Fig. 62).

Digestive System (Figs. 5, 7, 38, 39, 45–47, 56, 58, 63–74, 76, 77): oral tube length $\sim 1/2$ odontophore length; walls with circular muscles (Figs. 63, 64: mc); basal region with oblique fibers (Fig. 66: mj), originating gradually from dorsal surface, close to median line. Fibers running posteriorly towards both sides, inserting in ventral surface of odontophore. Jaw plates (Figs. 38, 39) thick, light brown, rounded, occupying half of buccal cavity dorsal surface. Minute denticles on ventral surface, starting on anterior portion and running obliquely towards ventral portion. Anterior edge denticulate, without true fringe. Pair of dorsal folds starting posteriorly to jaws (Fig. 73: df), with each fold bending and forming two partially overlapping rounded slits. Ventral slit triangular. Series of transverse muscles separating outer surface of esophagus from odontophore. Odontophore about twice longer than snout.

Odontophore muscles (Figs. 63–71): m1: series of small jugal muscles connecting buccal mass with adjacent inner surface of snout and haemocoel. m1d: pair of small dorsal jugal retractors, originating in postero-lateral region of mouth sphincter and inserting in antero-lateral edge of posterior cartilage. m1v: pair of small ventral jugal protractors of odontophore, originating on central surface of oral tube, running posteriorly away from each other and inserting in postero-ventral region of odontophore, in median surface of posterior cartilages. m4: broad pair of dorsal tensor muscles of radula and subradular membrane, originating partly in ventral surface of anterior cartilages, at some distance from median line, and partly in posterior lateral surfaces of posterior cartilages, surrounding lateral and ventral surfaces of anterior cartilages, with insertion along dorsal region of subradular membrane (exposed inside buccal cavity) and a portion in radular ribbon preceding buccal cavity. m5: pair of large accessory dorsal tensor muscles of radula, originating in ventral



FIGS. 71–78. Anatomy *Calliostoma adpersum*. FIG. 71: Left view of posterior region of odontophore, radular sac partially removed (scale bar = 1 mm); FIG. 72: External dorsal view of stomach and adjacent region of visceral whorls; FIG. 73: Buccal cavity, anterior and mid-esophagus opened longitudinally, ventral-inner views, odontophore removed; FIG. 74: Stomach opened longitudinally, ventral-inner view (scale bars = 2 mm); FIG. 75: Overview of nerve ring (scale bar = 1 mm); FIGS. 76, 77: Foregut and central nervous system, right and left sides (scale bar = 2 mm); FIG. 78: Topology of nervous system, frontal view (scale bar = 1 mm).

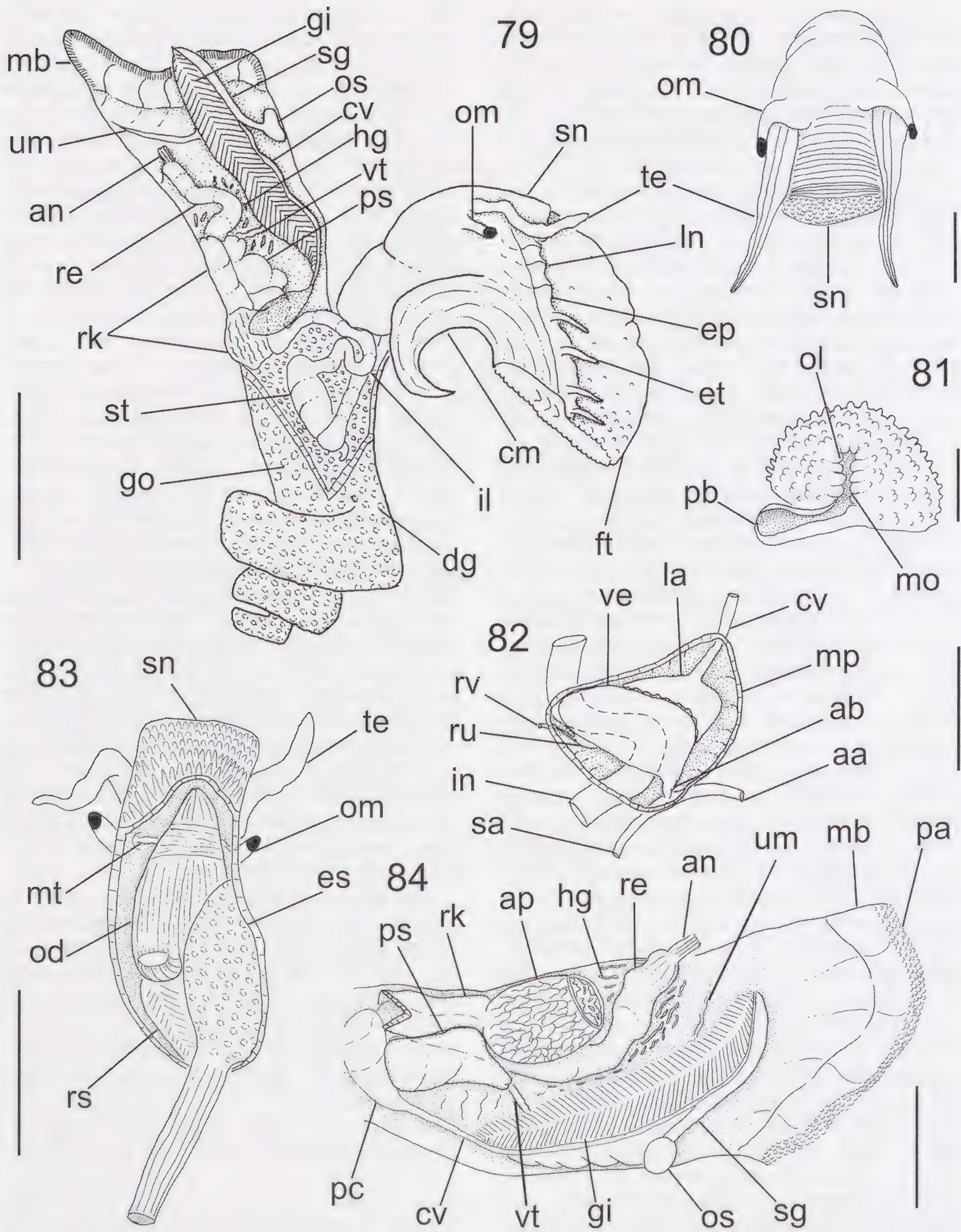
surface of posterior cartilages, running firstly towards dorsal and median and subsequently anteriorly, with insertion in region of radular ribbon. m6: horizontal muscle uniting almost entirely the ventral edges of the two anterior cartilages (excepting short posterior region on external surface). m7: very small, thin pair of muscles, originating on middle region of inner ventral surface of radular sac, running anteriorly and separating from one another at their middle level (insertion not observed). m7a: very small and thin pair of muscles, originating in haemocoelic ventral surface, running dorsally and separating from one another surrounding m7, with insertion in radular sac, posterior to insertion of m5. m7b: pair of muscles originating in lateral inner wall of radular sac, inserting in posterior cartilage. m8: pair of broad approximator muscles of cartilages, originating in anterior cartilages (along its lateral surface and posterior to insertion of mj), running posteriorly, decreasing gradually and inserting in middle region of anterior surface of posterior cartilages; m8a, pair of accessory muscles of m8, originating posteriorly in anterior cartilages on the opposite side of m8 origin, running parallel, covering m4 and inserting in antero-lateral region of posterior cartilages. m10: broad pair of ventral protractor muscles of odontophore, originating from ventral region of mouth and buccal sphincter, running posteriorly, inserting in anterior region of posterior cartilage, ventrally to m8 insertion. m11: pair of thin ventral tensor muscles of radula, originating in middle region of ventral surface of posterior cartilage (separated from one another by distance equivalent to their width), running anteriorly and covering m6 and ventral surface of anterior cartilage, becoming wider in anterior region and inserting in distal edge of subradular membrane. m11a; very long and thin pair of oblique ventral tensor muscles of radula, originating in haemocoelic anterior surface near pleural ganglia, running dorsally between anterior edge of anterior cartilages and inserting in subradular membrane distal edge. mj: originating gradually from dorsal surface close to median line, running divergently towards posterior and sides and inserting in ventral surface of odontophore. mt: single transversal muscle originating from lateral wall of haemocoel, running through ventral surface of odontophore under m10 and m1v and inserting into opposite wall.

Non-muscular structures of odontophore (Figs. 66–68): oc: pair of anterior cartilages,

antero-posteriorly elongated, flat, with anterior and posterior ends rounded and of same length of odontophore. po: small pair of posterior odontophore cartilages, of 1/10 of anterior cartilages length and located in posterior region, slightly lateral to anterior cartilages. br: subradular membrane covering most of the odontophore surface exposed in buccal cavity, where most of intrinsic odontophore muscles inserts. sc: subradular cartilage maintaining radular ribbon, expanding in buccal cavity beyond radula and covering about half the exposed portion of subradular membrane.

Radular sac wide, twice longer than odontophore. Posterior end of radular sac broadly bifid. Radula (Figs. 45–47) symmetrical, rows arched. Rachidian 1/9 of radula width, base rectangular; cutting edge with projection turned posteriorly (almost 90°) and covering posterior end of preceding tooth; tip narrowly tapered, finely serrated; interlock sub-terminal, at base of cutting projection. Four lateral teeth similar to rachidian but narrower and bent medially, forming curve with concave side towards radular sac; teeth sharply pointed, finely serrated, with about 25 secondary cusps separated from each other along both edges. About 30 marginal teeth; innermost pair greatly enlarged, with large base and coarsely serrate hooked cusps; secondary cusps curved, on inner surface twice size of cusps on outer surface. Succeeding inner marginals of similar built, but less massive. Outer marginals with delicate secondary cusps along both sides of tip; become more slender towards the edge of radula.

Inner surface of anterior esophagus with three food channels, two dorsal and one ventral (Fig. 73: df, vf), the latter bearing esophageal valve (Fig. 73: ev). Mid esophagus with three folds (two dorsal and one higher ventral) forming three shallow chambers; epithelium (Fig. 73: el, eg) entirely covered by villous papillae. Posterior esophagus (Fig. 56) narrow (but with enlarged posterior portion), with some thin longitudinal folds on inner surface. Stomach (Figs. 56, 72, 74: st) oval, very thin walled, taller than wide, occupying 1/4 of first whorl, divided into two parts, a more globular posterior and a more cylindrical anterior. Posterior part with two typhlosoles on left side (Fig. 74: ti) running into spiral caecum; gastric shield (Fig. 74: gs) a thin cuticle with 1/6 of stomach area, located on middle left side of posterior part. Spiral caecum (Figs. 72, 74: lc) with 1½ counter clockwise (in dorsal view) whorls. Esophageal insertion in posterior me-



FIGS. 79–84. Anatomy *Calliostoma depictum*. FIG. 79: Pallial cavity roof and visceral mass in ventral view, head-foot deflected to right (scale bar = 2 mm); FIG. 80: Head, anterior view; FIG. 81: Detail of anterior surface of snout, ventral view; FIG. 82: Pericardium, ventral-inner view, ventral walls and kidneys removed (scale bars = 1 mm); FIG. 83: Head and anterior digestive system, ventral view; FIG. 84: Pallial cavity roof, ventral-inner view (scale bars = 2 mm).

dian stomach region. Intestine origin in anterior end. Intestine (Fig. 56: in) very wide, running anteriorly forward next to haemocoel, bending abruptly and forming wide loop (Fig. 56: il); anterior region of visceral mass with small loop surrounding kidney and pericardium, exiting in right-posterior corner of pallial cavity. Rectum and anus described above (pallial organs).

Genital System (Figs. 6–8, 56): female with modified right kidney (described above). Brief histology: single epithelium with granular glandular cells; mesothelium composed of connective tissue and muscle fibers. Invagination of epithelium forming radial arrangement of trabeculae. Oogenesis: oogonia of 40 µm (Fig. 6: oo) attached to trabeculae, nucleus central; oocyte (Fig. 6: ov), under development, of 80 µm, pyriform, attached to trabeculae by peduncle, nucleus central; mature oocyte (Fig. 6: om) of 210 µm, surrounded by chorion layer, nucleus and nucleolus displaced from center. Spermatogenesis: germinative tissue attached to trabeculae; mature spermatocyte (Fig. 8: em) with spermatozoa distributed throughout testis as feathery bundles; acrosome, nucleus and flagellum not examined.

Central Nervous System (Figs. 67, 75–77): nerve ring surrounding anterior half of buccal mass. Cerebral ganglia rounded, located on lateral region of buccal mass (Figs. 76, 77: ce), occupying ~ 1/3 of its area; commissure thick, long, dorso-ventrally flattened; cerebropleural and cerebropedal (Figs. 76–78: cp, pm) connectives long, thin, originating in anterior region of cerebral ganglia and running ventrally and back to pedal and pleural ganglia. Labial ganglia (Figs. 76–78: lg) 1/3 of cerebral ganglia, located in ventro-lateral region of buccal mass, anteriorly to cerebral ganglia; connected to cerebral ganglia by short cerebrolabial connective (Fig. 75: cl). Buccal ganglia (Figs. 76, 78: bg) of same size as labial ganglia, posterior to cerebral ganglia; connected to cerebral ganglia by a buccolabial connective (Figs. 77, 78: bl). Buccal commissure thick (Fig. 67: bc, to), lying dorsally in relation to radular tissue. Pleural and pedal ganglia (Fig. 78: pe, pl) close to one another, inside pedal musculature immediately below ventral surface of haemocoel; both of about half size of cerebral ganglion. Pedal commissure thick, very short. Pedal nerve (Fig. 78: pd) running forward from each pedal ganglion, surrounding medial pedal blood

sinus. Supra-esophageal connective (Fig. 78: cs) emerging from right pleural ganglia. Sub-esophageal connective (Fig. 78: cb) emerging from left pleural ganglia. Statocysts (Fig. 78: ta) rounded, bright, located very close to posterior side of pedal ganglia.

Distribution

From Colombia to Brazil, Santa Catarina: 12.27°N to 27°S, 74.5°W to 29.3°W (Rosenberg, 2009).

Habitat

From 20 to 50 m depth, hard bottoms in western part of its range, sandy mud bottom in eastern and southern part.

Material Examined

Brazil: Espírito Santo: Vitória, MZSP 66724, 03 shells (iii/2000). Rio de Janeiro; Arraial do Cabo, MZSP 72425, 1 shell (P. Gonçalves col. i/2005); Búzios, Ossos Beach, 22°46'49.00"S, 41°53'09.82"W, MZSP 62544, 1 shell (Simone col. 18/i/1982); Angra dos Reis, Ilha Grande, MZSP 24110, 10 shells (De Fiore col.). São Paulo: Ubatuba, Boqueirão, MZSP 24111, 05 specimens (14/vii/1962); Anchieta Island, MZSP 26953, 01 specimen; Pesca and Selinha Islands, 23°23'S, 45°52'W, MZSP 38190, 01 specimen (BIOTA – FAPESP 11/vi/2001); Caraguatatuba, Ponta Grossa, 23°37'S, 45°24'W, MZSP 38196, 1 specimen (BIOTA – FAPESP 24/iv/2001); MZSP 38193, 2 specimens (BIOTA – FAPESP 16/x/2001); São Sebastião, MZSP 8958, 22 shells (Ihering col. 1896); Araçá, MZSP 24117, 11 specimens (15/ix/1962), Baraqueçaba Beach, MZSP 24118, 35 shells (E. Boffi col. xi/1969); Ilha-bela, Perequê, MZSP 63562, 2 specimens (Simone 05/vi/1993), MZSP 58934, 1 specimen (Amaral, C. col. 23/ix/1992); Santos, MZSP 71948, 1 shell (v/2004); Peruíbe, Central Beach, MZSP 62554, 3 shells (M. Borges col. 26/i/1982).

Calliostoma depictum

Dall, 1927

Figs. 9–23, 40–43, 48–50, 79–90

Calliostoma depictum Dall, 1927: 6. Rios, 1975: 23, pl. 6; Quinn, 1992: 110, figs. 101, 102, 122; Rosenberg, 2009.

Calliostoma (Kombologion) adpersum Philippi: Clench & Turner, 1960: 46–48, pl. 31; Rios, 1970: 25; Abbott & Dance, 2000: 38 (*non* Philippi, 1851).

Calliostoma (Neocalliostoma) depictum: Rios, 1985: 22, pl. 10, fig. 89.

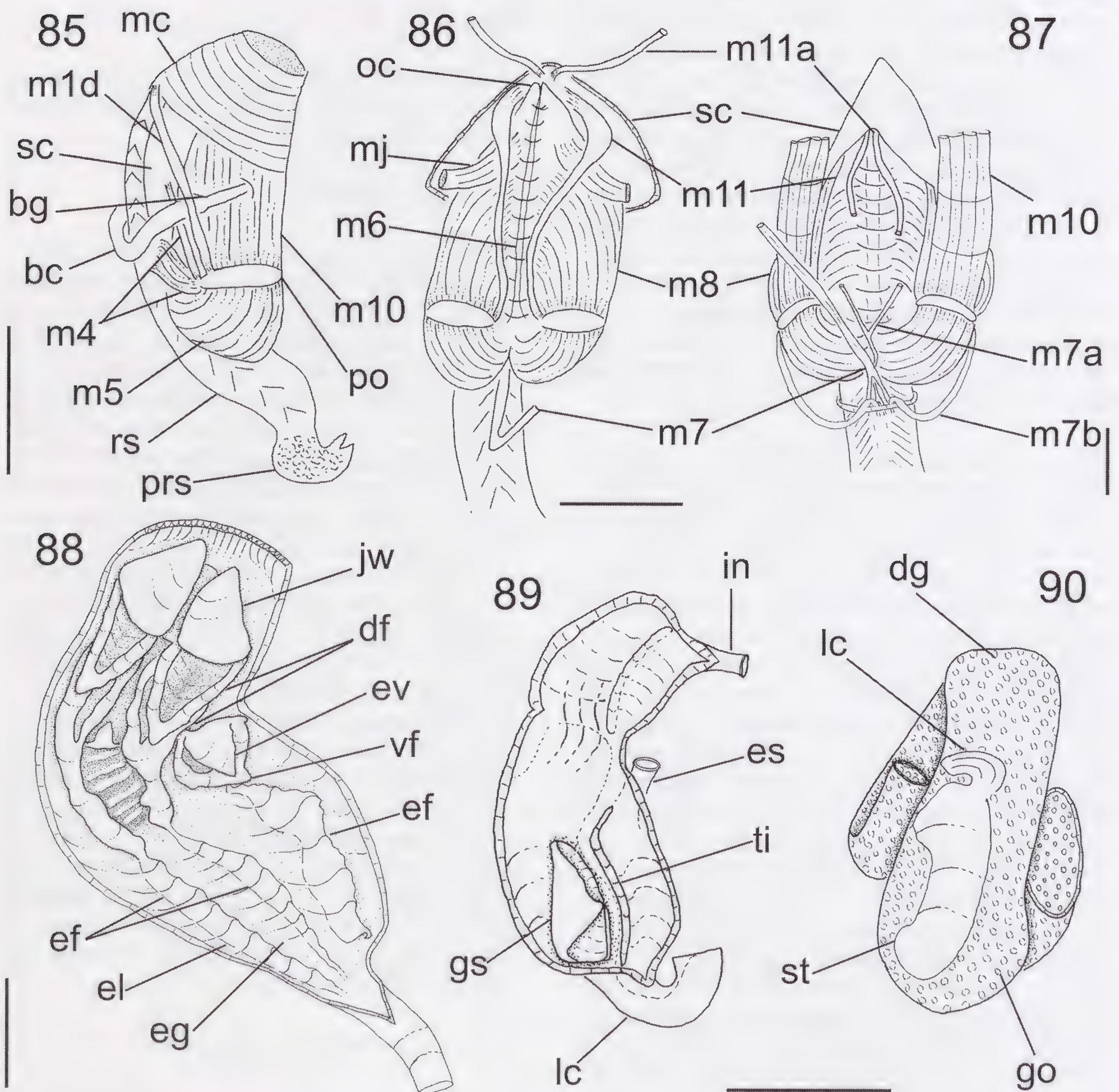
Calliostoma (Emerlinia) depictum: Rios, 1994: 33, pl. 33, fig. 91; 2009: 49, fig. 107.

Type Material: Holotype NMNH 152667 (examined).

Type Locality: Brazil, Bahia State.

Diagnosis

Turbiniform shell, suture distinct. Sculptured by beaded fine threads. Spots of reddish purple color on cords of teleoconch and base. Marked groove near columella. Foot reddish brown. m8a odontophore muscle absent. Ventral esophageal fold slightly larger than dorsal folds. Spiral caecum with 1/2 whorl.



FIGS. 85–90. Anatomy *Calliostoma depictum*. FIG. 85: Buccal mass, right view, anterior and mid-esophagus extracted; FIGS. 86, 87: Odontophore, ventral view. FIG. 86: Subradular cartilage opened longitudinally and deflected, m10 removed; FIG. 87: m10 deflected to show inner structures; FIG. 88: Buccal cavity, anterior and mid-esophagus opened longitudinally, ventral-inner views, odontophore removed (scale bars = 1 mm); FIG. 89: Stomach opened longitudinally, ventral-inner view; FIG. 90: External dorsal view of stomach (scale bars = 2 mm).

Comparative Description

Shell (Figs. 9–18): size ~ 8 mm in height and diameter; 5–6 convex whorls; spire angle ~ 80°. Turbiniform, imperforate, with marked groove near columella (Fig. 13). Color pale with large reddish purple or reddish pink axial patches; some reddish brown or purple spots on cords of teleoconch and base. Apex very dark brown. Protoconch (Figs. 40, 41) of about 1 whorl; structure not observed. Umbilical area white. Suture deep. Teleoconch with spiral beaded cords; last adult whorl and base with 11 cords, smoother at base; delicate and thin (Fig. 40) ribs in first whorl. Aperture subquadrate, prosocline (~ 40° with columellar axis). Juvenile specimens (Figs. 15, 16) with flattened whorls; colored spots only in innermost line of base. More details in Dall (1927) and Quinn (1992).

Head-Foot (Figs. 17, 18, 79–81): rounded head; snout wide, cylindrical, red-brown, papillated. Outer lip of mouth with pseudoproboscis. Pair of cephalic lappets absent. Cephalic tentacles asymmetrical with each other; dorsal-ventrally flattened, grooved, twice snout length; red brown with darker median strip, white near base. Ommatophore reddish, of about 1/4 the length of cephalic tentacles. Eyes dark, round, occupying anterior edge of ommatophore. Foot strongly reddish brown colored; papillae white. Fewer papillae than preceding species. Opercular pad located in the middle of dorsal region. Barely noticeable chevrons on dorsal region. Furrow of pedal glands along entire anterior edge of foot. Symmetrical neck lobes, with smooth edges. Epipodium with four pairs of tentacles, inserted sub-terminally at its distal edge; tentacles similar in size.

Operculum (Figs. 20, 21): as in preceding species, but brownish silvery, very thin, with 3 mm in diameter and up to 14 whorls.

Mantle Organs (Figs. 79, 84): gill with half palial cavity length and 1/4 of its width, extended anteriorly by wide suspensory membrane. Afferent gill vessel of almost same length as gill. Ctenidial vein 20% longer than gill, free from gill filaments, located left of afferent vessel up to pericardium. Hypobranchial glands (Fig. 84: hg) white, slightly thicker in females. Rectum thick, sigmoid, occupying 2/3 of cavity length. Kidneys 1/3 rectum length. Right kidney modified on females.

Visceral Mass (Figs. 79, 90): similar to preceding species.

Circulatory and Excretory Systems (Figs. 79, 82, 84): ventricle 1/2 of pericardium volume; left auricle 1/4 of pericardium; right auricle ~ 1/5 of left auricle. Vessels as preceding species. Papillary sac 1/3 of rectum length and twice its width. Anterior right kidney with same size of papillary sac on males. Ampulla, on females, with twice the width of papillary sac. Posterior right kidney as preceding species.

Digestive System (Figs. 19, 42, 43, 48–50, 79, 83, 84–90): oral tube (Figs. 85, 86) walls with circular muscles and jaw muscles on basal region. Jaws triangular in shape (Figs. 19, 42, 43); denticles long, without true fringe, on distal edge. Odontophore partially covered by mid-esophagus in ventral view (Fig. 83). Odontophore muscles (Figs. 85–87): m1; m1d; m1v; m4; m5; m6; m7; m7a; m7b; m8; m10; m11; m11a; mj; mt; ef. Radula (Figs. 48–50): rachidian 1/9 of total width; stem wide; cutting edge triangular with projection turned posteriorly (almost 90°); tip tapered, with finely small secondary cusps on both sides. Five lateral teeth with wide bases and very thin stems (1/10 of base width). About 25 marginal teeth. Innermost marginal (Fig. 50) greatly enlarged with heavy three secondary cusps. Other marginals with delicate secondary cusps along both sides of tip; becoming more slender towards the outside.

Buccal cavity and anterior and posterior esophagus similar to preceding species: anterior esophagus with three food channels, two dorsal and one ventral, continuing to mid esophagus (Fig. 88: ef); ventral esophageal fold slightly larger than dorsal folds. Stomach ~ 1/2 visceral mass width (Fig. 90); central region depressed; with two typhlosoles, one on left side of posterior area, other on left side of anterior area. Gastric shield (Fig. 89: gs) thicker than in *C. adspersum*. Spiral caecum 1/2 whorl counter clockwise (Fig. 89: lc). Intestine similar to preceding species.

Genital System (Figs. 22, 23): sexual dimorphism by ampulla on female (see above). Gonad with single epithelium above layer of connective tissue and muscle fibers, forming radial arrangement of trabeculae. Oogenesis: oogonia and oocyte attached to trabeculae, nucleus central; mature oocyte displaced from trabeculae and surrounded by chorion layer,

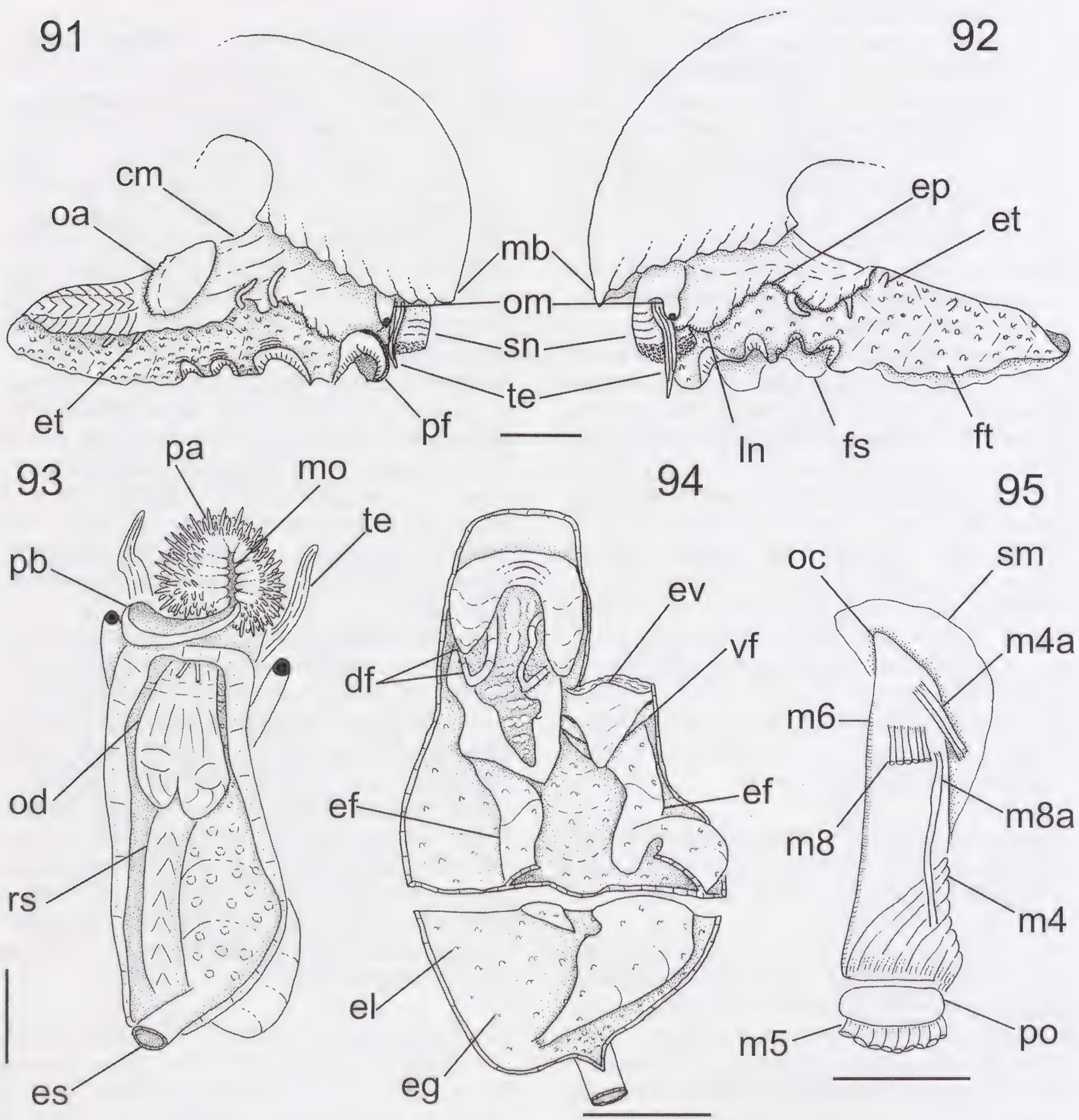
nucleus and nucleolus displaced from center. Spermatogenesis: germinative tissue attached to trabeculae and spermazoa feather-like.

Central Nervous System: nerve ring located on anterior half of buccal mass. Cerebral ganglia rounded, dorso-ventrally flattened. Cerebropleural connective twice as thick as cerebropedal connective. Labial ganglia 1/5 of cerebral ganglia; cerebrolabial connective as

thick as cerebropleural. Buccal ganglia slightly larger than labial ganglia; buccal commissure thick. Pleural and pedal ganglia close to one another; connective imperceptible. Statocysts rounded, bright.

Distribution

Brazil, Maranhão to São Paulo: 13°S to 23°S, 43°W to 29.3°W (Rosenberg, 2009).



FIGS. 91–95. Anatomy *Calliostoma hassler*. FIG. 91: Head-foot and adjacent region of mantle in right view; FIG. 92: Same in left view (scale bars = 4 mm); FIG. 93: Head and anterior digestive system, ventral view, foot removed; FIG. 94: Buccal cavity, anterior and mid-esophagus opened longitudinally, ventral-inner views, odontophore removed; FIG. 95: Odontophore, left side in lateral view, m8 and m10 removed, subradular membrane and m5 deflected (scale bars = 2 mm).

Habitat

From 1 to 7 m, in sandy areas around rocks and coral. Often found below sea urchins.

Material Examined

Holotype: NMNH 152667.

Brazil: Rio Grande do Norte: Rio do Fogo, MZSP 84265, 1 shell (M. Coltro, col. i/2007). Bahia; MZSP 56354, 1 shell; Salvador, MZSP 71951, 1 shell (B. Linhares col. xi/1998), MZSP 66727, 2 shells (B. Linhares col. vii/1998), Farol da Barra Beach, MZSP 81797, 3 shells (Simone col. 22–28/ii/1997). Rio de Janeiro: Cabo Frio, Papagaio Island, 22°46'S, 41°53'W, MZSP 92320, 11 specimens (Dornellas col. 14/ix/2009); Arraial do Cabo, Saco do Cherne, 22°53'37.6"S, 41°59'13.8"W, MZSP 92318, 1 specimen (Dornellas col. 15/ix/2009), Forno Beach, MZSP 92413, 1 specimen (Dornellas col. 18/ix/2009); Angra dos Reis, Jorge Grego Island, 23°13'S, 44°08'W, MZSP 91749, 27 specimens (Dornellas & Amaral col. 08/viii/2009). São Paulo: São Sebastião, Ilhabela, Cabras Island, 23°49'S, 45°23'W, MZSP 41575, 9 specimens (Simone et al. col. 06/v/2004); Alcatrazes Island, Faroleiros Harbor, MZSP 28322, 2 specimens (Simone col. 29/xi–01/xii/1996); Santos, Embaré Beach, MZSP 84604, 1 shell (Simone col. 1978); Itanhaém, Queimada Pequena Island, MZSP 84887, 4 specimens (Dornellas et al. col. 01/iii/2007).

Calliostoma hassler

Clench & Aguayo, 1939

Figs. 24–35, 44, 51–53, 91–98

Calliostoma (Astele) hassler Clench & Aguayo, 1939: 191, pl. 28, fig. 3.

Calliostoma hassler – Clench & Turner, 1960: 66–67, pl. 48; Rios, 1970: 25, pl. 5; 1975: 24, pl. 6, fig. 64; 1994: 34, pl. 10, fig. 101; 2009: 51, fig. 114; Abbott & Dance, 1986: 38, fig.; Rosenberg, 2009.

Calliostoma (Elmerlinia) bullisi Clench & Turner – Rios, 1970: 24, pl. 5 (*non* Clench & Turner, 1960).

Calliostoma barbouri Clench & Turner – Rios, 1975: 23, pl. 5, fig. 60 (*non* Clench & Aguayo, 1946).

Calliostoma (Neocalliostoma) hassler – Rios, 1985: 22, pl. 10, fig. 91.

Calliostoma vinosum Quinn, 1992: 96, figs. 53–56, 114; Rios, 2009: 53, fig. 118, syn. nov.

Type Material: *Calliostoma hassler* Holotype in MCZ 104554. Paratypes in MCZ 104555 and Museo Poey; *Calliostoma vinosum* Holotype in MORG 29.294. Paratypes in USNM 860256; FSBC I 44067; MORG 15.043.

Type Locality: Brazil, Rio de Janeiro off Cabo Frio.

Diagnosis

Shell with rounded peripheral keel. Foot strongly reddish brown colored, densely papillated on dorsal region. Rachidian slender, with two pronounced flaps on its base. Two esophageal folds. Intestine forming two wide loops; spiral caecum absent.

Comparative description

Shell (Figs. 24–35): up to 25 mm in height and diameter and eight slightly convex whorls; spire angle ~ 65°. Trochoid, flat sided, finely sculptured, with rounded peripheral keel. Umbilicus deep. Color light reddish brown with yellowish white axial blotches. Base with white colored spots on cords. Protoconch of one whorl, light-colored. Umbilical area yellowish to white. Sculptured by beaded spiral cords; last adult whorl and base with 15 cords; inner cord on base stronger than the others. Suture indistinct. Aperture subquadrate, prosocline (~ 45° with columellar axis of shell). Columella arched, not truncate at base, forming slight callus. Juvenile specimens (Figs. 26, 27, 30, 31, 34, 35) with flatter whorls and without rounded peripheral keel.

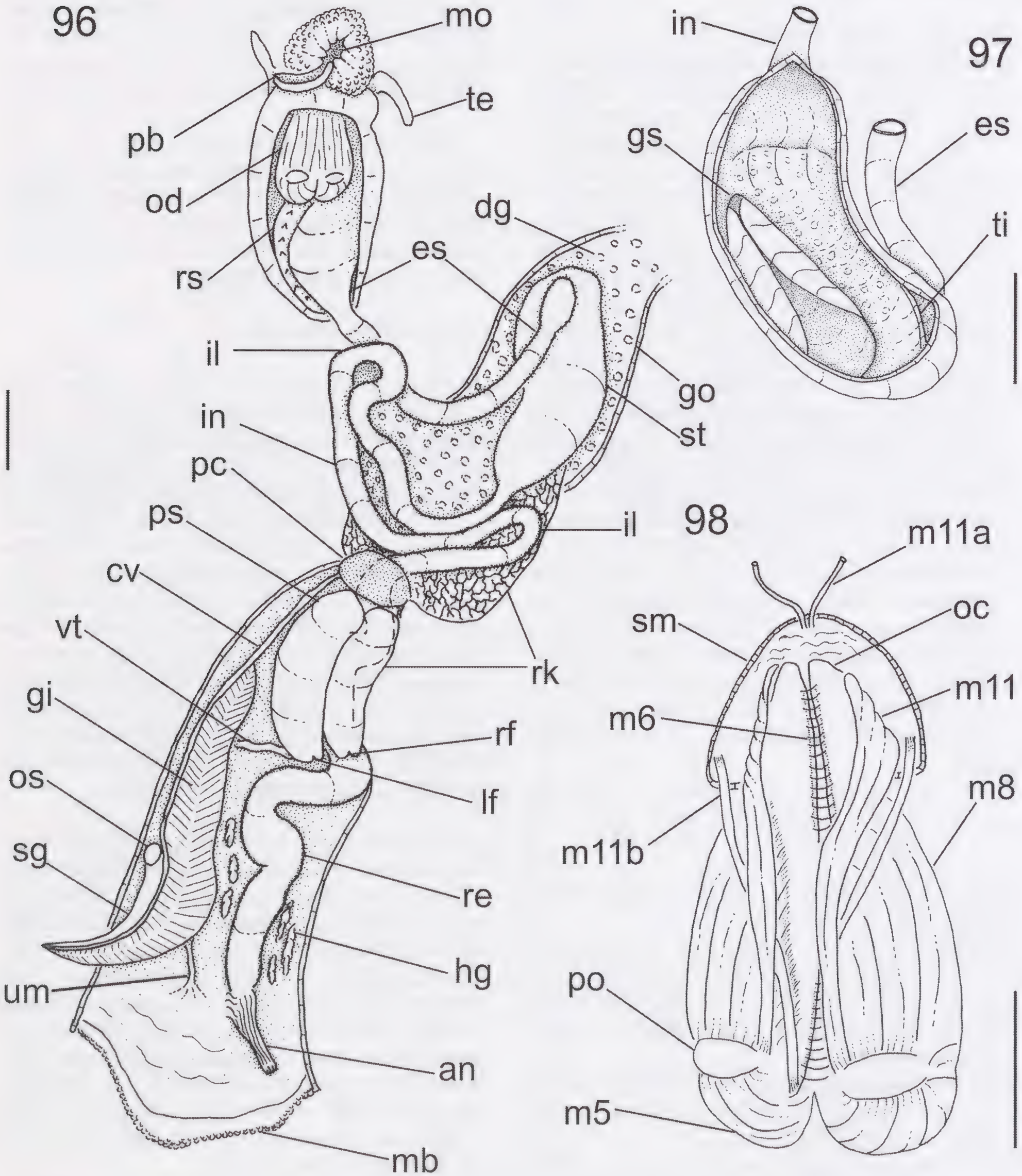
Head-Foot (Figs. 91–93): snout 1/3 of head-foot width; distal end densely papillated; outer lip with pseudoproboscis. Cephalic lappets absent. Cephalic tentacles dorsal-ventrally flattened, grooved, covered by small papillae. Ommatophore 1/3 of tentacles length. Foot brown with numerous white papillae on dorsal region; posterior end (Fig. 91) light brown with chevrons and two tall longitudinal furrows. Neck lobes asymmetrical: left lobe finely digitated; right lobe with smooth edge. Epipodium with 4 pairs of tentacles (Figs. 91, 92: et), nearly equidistant to each other.

Operculum: similar to *C. adpersum*. 12 whorls and 8 mm in diameter.

Mantle Organs (Fig. 96): gill with more than half of pallial cavity width; afferent vessel ~ 2/3 gill

length. A quarter of the ctenidial vein free from gill filaments. Hypobranchial glands thin, white. Rectum thick, sigmoid, occupying almost entire cavity length.

Visceral Mass (Fig. 96): 1/4 of first whorl and remaining whorls. Otherwise similar to preceding species.



FIGS. 96–98. Anatomy *Calliostoma hassler*. FIG. 96: Pallial cavity roof, visceral mass, head-foot deflected, ventral-inner views; FIG. 97: Stomach opened longitudinally, ventral-inner view; FIG. 98: Odontophore, ventral view, subradular cartilage opened longitudinally and deflected, m10 and radular sac removed. Scale bars = 2 mm.

Circulatory and Excretory Systems (Fig. 96): pericardium not examined. Papillary sac and anterior right kidney 1/3 of rectum length and same width. Posterior right kidney as in preceding species.

Digestive System (Figs. 44, 51–53, 93–98): oral tube walls with circular muscles; jaw muscles on basal region. Jaws (Fig. 44) triangular in shape, dark brown; very long denticles on anterior end, projected in tufts. Odontophore muscles (Figs. 95, 98) similar to preceding species (except for m11b): m1, m1d, m1v, m4, m5, m6, m7, m7a, m7b, m8 and m8a as in *C. adpersum*; m10, m11, m11a, mj, mt. Muscle m11b: thin ventral pair of radular muscles originating in dorsal surface of posterior cartilage, running parallel to m11 and inserting itself in ventral surface of anterior region of subradular membrane. Radula (Figs. 51–53): rachidian 1/10 of total radula width, with very large nearly triangular base and narrow stem. Six lateral teeth, with base larger and stem shorter from those of preceding species; two outer teeth modified in lateromarginal plates. About 30 marginal teeth; innermost teeth similar to *C. adpersum*, remaining teeth similar to one another; secondary cusps becoming slender and larger; central cusp rounded.

Buccal cavity and esophagus similar to both preceding species, except for mid esophagus with two esophageal folds (Fig. 94: ef): a higher ventral fold and a right dorsal fold. Stomach (Fig. 97) without spiral caecum; one typhlosole on left side of posterior area; gastric shield similar to *C. depictum*. Intestine longer than in preceding species; following same route, but forming two wide loops (Fig. 96: il). Anus wider.

Genital System: not examined.

Central Nervous System: cerebral ganglia rounded; commissure long, thick, dorso-ventrally flattened. Cerebropleural connective ~ 1/3 cerebropedal width. Labial ganglia ~ 1/5 cerebral ganglia; cerebrolabial connective short. Buccal ganglia about same size as labial ganglia; buccal commissure thick. Pleural and pedal ganglia not observed.

Distribution

Venezuela to Rio de Janeiro, Brazil: 4°N to 23°S, 63°W to 32°W (Rosenberg, 2009).

Habitat

From 20 to 100 m; living on bottoms where bryozoans and coralline algae are abundant (Clench & Turner, 1960).

Material Examined

Brazil: Bahia; Belmonte, MZSP 37264, 3 specimens (A. Bodart col. vii/2003); Alcobaça, MZSP 34885, 11 specimens (Coltro leg.). Espírito Santo; Guarapari, 5 specimens (vi/2006), MZSP 69424, 09 specimens (A. Bodart col. v/2004), MZSP 57485, 9 specimens (Coltro leg. iv/1992).

DISCUSSION

The anatomy of *Calliostoma adpersum*, *C. depictum* and *C. hassler*, as well as *C. zizyphinum* (Linnaeus, 1758), *C. jujubinum* (Gmelin, 1791) and *C. tupinamba* Dornellas, 2012 (Dornellas, 2012; Fretter & Graham, 1962; Sá & Coelho, 1986), when compared with other morphological studies on trochoids or vetigastropods, revealed unique anatomical particularities. As such, the particularities of *Calliostoma* according to some authors (Randles, 1905; Fretter & Graham, 1962), and corroborated here, are: presence of ampulla in female (Figs. 84, 56: ap); reduction or lack of cephalic lappets (Figs. 55, 80); presence of pseudoproboscis (Figs. 81, 93: pb). Most vetigastropods have an intestinal loop inside the head-foot haemocoel, but in this study, we observed it outside of the haemocoel (Figs. 56, 79, 96: il). The absence of visceral structures in haemocoel is considered a synapomorphy of Caenogastropoda (Simone, 2011) and is, then, a convergent character that Caenogastropoda share with *Calliostoma*. A typical radular pattern characteristic of Calliostomatinae consists of thin, highly flexible teeth with fine, serrate cusps (Hickman & McLean, 1990), a modified innermost marginal tooth with a heavy base and coarsely serrate hooked cusp (Fig. 50), and the remaining lateral marginal teeth gradually decrease in size.

Nevertheless, the conchological characters lack any attribute that can be considered unique. Despite this, the identification of *Calliostoma* is relatively easy. The trochoid shape, flattened or slightly convex whorls, beaded spi-

TABLE 1. Morphological differences of the shells, jaws and radulae between the three species of *Calliostoma*.

Shells, jaws and radulae attributes	<i>C. adspersum</i>	<i>C. depictum</i>	<i>C. hassler</i>
Whorls	somewhat flattened	rounded convex	slightly convex
Peripheral keel	flattened	without a keel	rounded
Umbilicus	imperforate	imperforate	perforate
Umbilical chink	absent	present	absent
Ontogenetic differences	absent	present	present
Jaws	rounded without a true fringe	pointed without a true fringe	pointed with a true fringe
Lateromarginal plate	absent	absent	present
Lateral teeth	5	4	4

ral cords sculpture, presence of axial blotches, and a subquadrate aperture are also present in other trochoid taxa (Hickman & McLean, 1990; Rios, 1994, 2009). The shell attributes allow the identification of the *Calliostoma* species (Table 1), but they cannot be neatly grouped as genera or subgenera as there are a wide variety of intermediate characters (Marshall, 1995a).

It is possible to detect different conchological patterns during development in *C. depictum* and *C. hassler*. The juveniles of both species have flat whorls (Figs. 15, 16, 26, 27, 30, 31, 34, 35), and the adults of *C. hassler* have a round keel, with a more round profile on the last (Figs. 24, 25, 28, 29, 32, 33). Shells of *C. depictum* have round convex whorls with colored spots on the base and the teleoconch. The juveniles of *C. depictum* have similar spots (Figs. 9–14), found only in the innermost line of the base. These ontogenetic stages are observed in populations of both species and because of this, we conclude that *C. vinosum* (Figs. 26, 27) is in fact a young *C. hassler*. The uniformity of anatomical patterns (discussed below) also confirms that they are the same species, as specimens identifiable as both were studied. *Calliostoma vinosum* is based only on conchological and external morphological features (Quinn, 1992), and was only compared with *C. barbouri* Clench & Aguayo, 1946, with no mention to *C. hassler*.

According to some authors, the neck lobe (Fig. 54: ln) of Trochidae is asymmetrical, one neck lobe has a smooth edge and the other with a digitated edge, or one is larger than the other, as is observed in species of *Tegula* Lesson, 1835; *Gibbula* Risso, 1826; and *Anti-*

margarita Powell, 1951 (Randles, 1905; Righi, 1965; Aldea et al., 2009). Symmetrical neck lobes and four pairs of epipodial tentacles are observed in *Calliostoma* species (Randles, 1905; Fretter & Graham, 1977), but an asymmetrical neck lobe was observed in *C. hassler* (Table 2) and many others calliostomatids from western Atlantic, New Zealand and New Caledonia (Quinn, 1992; Marshall, 1995a, b). Four pairs of epipodial tentacles are not unique to *Calliostoma*, and they occur similarly in *Tegula* and *Astraea* Bolten, 1798 (Turbinidae) (Righi, 1965; Monteiro & Coelho, 2002; personal observation).

The pallial organs in *Calliostoma* differ from other vetigastropods by the presence of the ampulla in females (Figs. 84, 56: ap). The hypobranchial glands of females in *C. adspersum* (Fig. 5: hg) are more development and orange. The function of these glands is still not understood. It seems to be associated with the production of an egg ribbon and defensive against possible predators (Fretter & Graham, 1962; Bryan et al., 1997; Harasewych, 2002). In a behavioral study on defense in *Calliostoma canaliculatum* (Lightfoot, 1786), the hypobranchial gland released a viscous yellow substance (Bryan et al., 1997). It should be noted that this colored gland was observed only in females of *C. adspersum*.

The ampulla, also known as urogenital papilla (Hickman, 1992), was described for *C. zizyphinum* by Perrier (1889) and is expanded to the right nephrostome and projected forward and located in a more anterior level than the left nephrostome. Some authors suggest that this structure is unique for the genus (Randles,

TABLE 2. Morphological differences of the soft parts between the three species of *Calliostoma*.

Soft parts attributes	<i>C. adpersum</i>	<i>C. depictum</i>	<i>C. hassler</i>
Neck lobe	symmetrical	asymmetrical	asymmetrical
Orange hypobranchial gland on female	present	absent	absent
m8a	present	absent	present
m11b	absent	absent	present
Esophageal folds	3	3	2
Ventral esophageal fold <i>versus</i> dorsal fold	ventral fold twice as larger	same size	ventral fold twice as larger
Spiral caecum, whorls	1.5	0.5	0
Large intestinal loop	1	1	2

1905; Fretter & Graham, 1962; Sá & Coelho, 1986). The ampulla was observed in *C. jujubinum*, *C. tupinamba* and here in *C. depictum* and *C. adpersum*, but not observed in *C. hassler*. We attribute this to preservational quality and not as an inherent character to *C. hassler*. A modified right kidney on females is present in other vetigastropods, *Gibbula* and *Monodonta* Lamarck, 1799, showed a tumid, fringed edge at the right nephrostome, called rosette (Randles, 1905; Fretter & Graham, 1962; Andrews, 1985). Although Righi (1965) mentioned an ampulla for *Tegula viridula* (Gmelin, 1791), its nephrostome most resembles the rosette, and it is on the same level of the left nephrostome in *T. viridula* and in *Astraea* (Monteiro & Coelho, 2002). On the other hand, some species of *Pleurotomaria* J. Sowerby, 1821, (*Pleurotomarioidea*) have a right nephrostome similar to that of *Calliostoma* ampulla. This structure is named the oviduct by Woodward (1889).

In a review of the western Atlantic *Calliostoma*, Clench & Turner (1960) assigned *C. adpersum* to the subgenus *Kombologion* Clench & Turner, 1960, and diagnosed the subgenus based on jaw and radula attributes (Table 1 shows differences among the three species). Those authors did not assign *C. hassler* to any subgenus, as neither the morphology of the jaws nor the radulae were known. *Calliostoma depictum* was placed in the subgenus *Elmerlinia* Clench & Turner, 1960, by Rios (1994), but its jaw and radula are not like those described for that subgenus (Clench & Turner, 1960: 4–6). Compared to other species, the jaw and radula of *C. hassler* (Fig. 53) appear more similar to those of *C. jujubinum* (allocated in *Elmerlinia*), differing by marginal teeth that do not change along the row. According to the subgenera de-

scriptions by Clench & Turner (1960), there is no one to properly attribute to *C. depictum*.

The odontophore muscles do not differ greatly among the species studied. The m8a (Figs. 68, 69, 95) is only present in *C. hassler* and *C. adpersum*. m11b appears to be exclusively found in *C. hassler* (Fig. 98) and *C. tupinamba*. It should be noted that there is little knowledge on the odontophore of trochoids, since only a few species were studied at this detail (e.g., Fretter & Graham, 1962; Righi, 1965; Simone & Cunha, 2006; Dornellas, 2012), and there are no studies of *Calliostoma* odontophores. At this time, the m1d, m7b and m11a pairs are exclusive to *Monodonta lineata* (da Costa, 1778), *Tegula viridula* and *Calliostoma* (Fretter & Graham, 1962; Righi, 1965), and the m1v is unique to *Gaza* Watson, 1879, and *Calliostoma* (Simone & Cunha, 2006). More research is needed into odontophore anatomy in *Calliostoma*, as well as in other trochoids.

As usual for vetigastropods, the odontophore cartilages of *Calliostoma* has two pairs of cartilage which consist of anterior and posterior pairs. The posterior cartilage is smaller than anterior cartilage and normally is not fused or overlapped, connected by approximator muscles of cartilage (m8). This conformation of cartilage indicates a plesiomorphic condition for gastropods (Katsuno & Sasaki, 2008).

Radula analysis is very useful in the diagnosis of subgenera in *Calliostoma* and at the species level (Clench & Turner, 1960; Castellanos & Fernandez, 1976; Marshall, 1995a, b; Quinn, 1992). The differences between *C. adpersum* and *C. depictum* radulae are described by Quinn (1992: 110) and are supported here. *Calliostoma depictum* has a more broadly cusped rachidian and has fewer pair of lateral

teeth (4 vs. 5, respectively) than *C. adspersum*. Additionally the rachidian have a narrower base and stem of lateral teeth in *C. adspersum* than in *C. depictum* (Figs. 46, 49). The number of marginal teeth reported by Quinn (1992), about 40 versus about 25, is not absolute, once a small difference between these numbers, about 30 versus about 25, can overlap. The radula of *C. hassler* resembles that of *C. jujubinum* (Clench & Turner 1960: pl. 5, fig. 2), but the marginal teeth (Fig. 53) are less different from their neighboring teeth along the row.

The enlarged mid-esophagus of trochids, as well as in other groups of gastropods, is usually composed of esophageal folds which compartmentalize this region, thereby increasing the area of food processing (Fretter & Graham, 1962; Salvini-Plawen & Haszprunar, 1987; Salvini-Plawen, 1988; Sasaki, 1998). The presence of papillate glands (Figs. 73, 88, 94: el, eg) covering the inner wall in this region is one of the main morphological synapomorphies of the clade Vetigastropoda (Haszprunar, 1988; Salvini-Plawen, 1988; Sasaki, 1998). For the mid-esophagus (Table 2), the number of esophageal folds is different in each species. Both *C. depictum* and *C. adspersum* have two dorsal and one ventral fold, being the ventral fold twice larger in *C. adspersum* (Figs. 73, 88: ef), also observed in *C. tupinamba* and *C. zizyphinum*. On the other hand, *C. hassler* has the mid-esophagus with only one dorsal and one ventral fold, which is as large as that in *C. adspersum*. The mid-esophagus of other trochids, as *Tegula viridula* and *Gaza compta* (Simone & Cunha, 2006), and the turbinids, *Astraea latispina* (Philippi, 1844) and *A. olfersii* (Philippi, 1850) is formed by four esophageal folds, two dorsal and two ventral (Righi, 1965; Monteiro & Coelho, 2002; Simone & Cunha, 2006). Currently, this aspect of three esophageal folds seems to be unique for *Calliostoma* and an important character for defining species. Fretter & Graham (1962) demonstrated the importance of a highly detailed study of the stomach anatomy. The proximal portion of the stomach possesses the gastric shield, a chitinous cuticle structure, and it is also characterized by the presence of two folds (typhlosoles). The distal portion is a narrow chamber laying the intestine (Strong, 2003).

The caecum is widely variable among basal gastropods. It varies from a small, crescent shape to a large, spiral sorting-area structure. The large spiral caecum is considered derived within Vetigastropoda. This structure opens

ventrally on the posterior end of the stomach, more or less as continuous extensions of the typhlosoles (Strong, 2003).

Nevertheless, a tendency for disappearance of the spiral caecum (Figs. 74, 89: lc, 97) in *C. adspersum*, *C. depictum* and *C. hassler* was observed, with 1.5, 0.5, and 0 whorls, respectively. *C. zizyphinum* and *C. jujubinum* are more similar to *C. adspersum*, with 1.5 whorls (Randles, 1905; Fretter & Graham, 1962; Sá & Coelho, 1986). Although the number of whorls may vary among species (e.g., there are 4.5 to 6 whorls in *Astraea latispina*, and 3 to 4.5 whorls in *A. olfersii*; Monteiro & Coelho, 2002), the loss of this structure at this level has never been reported. According to Fretter & Graham (1962), the absence or vestigial spiral caecum is found only in advanced gastropod groups. In fact, and pertinent to the midgut observations, it should be noted that the preservation of the visceral mass of trochids depends on techniques rarely used in ordinary collections (Simone & Cunha, 2006; personal observation). It consists basically of making a small incision in the apical portion of the shell in order to allow the alcohol to be absorbed throughout the body. In the absence of these procedures, the study of these structures is difficult. Therefore, we believe there may be some vestigial spiral caecum in the stomach of *C. hassler* where the spiral caecum is not projected outside, somewhat similar to *Monodonta lineata*, (Fretter & Graham, 1962).

The intestine of the studied *Calliostoma* species differs from other trochids (Monteiro & Coelho, 2002; Sasaki, 1998; Simone, 1998) by lacking an intestinal loop (Figs. 56, 79, 96: il) within the head-foot haemocoel. In these species, and in more derived caenogastropods (Simone, 2004, 2005, 2011), there is no intestinal loop or visceral organs in the haemocoel. In *C. hassler* (Fig. 96: il), the intestine has two long intestinal loops, and is longer in proportion when compared to other species.

The only dimorphism in the genital system is in the ampulla of females (as discussed above). Histologically, the gonads of *C. adspersum* and *C. depictum* (Figs. 6–8, 22, 23) are similar to the other gonocoristic prosobranchs, which have only one epithelium and a trabecular system (Collado et al., 2008; Ortiz-Ordoñez et al., 2009).

A ventral position of the pair of pleural ganglia near the pedal ganglion (Fig. 78: pl, pe) is referred to as a hypoathroid condition in the nervous system. This condition is typical in veti-

gastropods (Fretter & Graham, 1962; Ponder & Lindberg, 1996, 1997). The central nervous system of *Calliostoma* is not differentiated among the species and demonstrates the similar pattern of other trochoids (Sasaki, 1998).

Based on anatomical evidence, *C. depictum* is not a synonym of *C. adpersum*, as was advocated by Quinn (1992). Many attributes separating *C. depictum* from other species, mainly conchological ones. Divergent features are the very convex whorls, distinct suture, and a marked groove near the columella. Soft parts differ in the following ways: an odontophore partially covered by the mid-esophagus (Fig. 83), the absence of the pair of odontophore muscles m8a, a ventral esophageal fold of the same size as the dorsal folds (Fig. 88: ef), and a reduced spiral caecum (Fig. 89: lc) with 0.5 whorl. Additionally, *C. depictum* is often found protected below sea urchins (Quinn, 1992; personal observation); there is no record of such behavior for *C. adpersum*.

As stated above, *C. vinosum* is a synonym of *C. hassler*, because specimens identifiable as both species were shown as a single ontogenetic series. Similar ontogenetic patterns are observed in *C. depictum*. Furthermore, specimens identifiable as *C. hassler* and *C. vinosum* lack the left dorsal esophageal fold, a gastric spiral caecum and an intestine forming two wide loops.

This study demonstrates that soft part features are essential for distinguishing *Calliostoma* species and for answer taxonomic questions that may not be resolved using shell and radula characters. The technique used herein can be applied towards understanding the taxonomy of more species in calliostomatids.

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